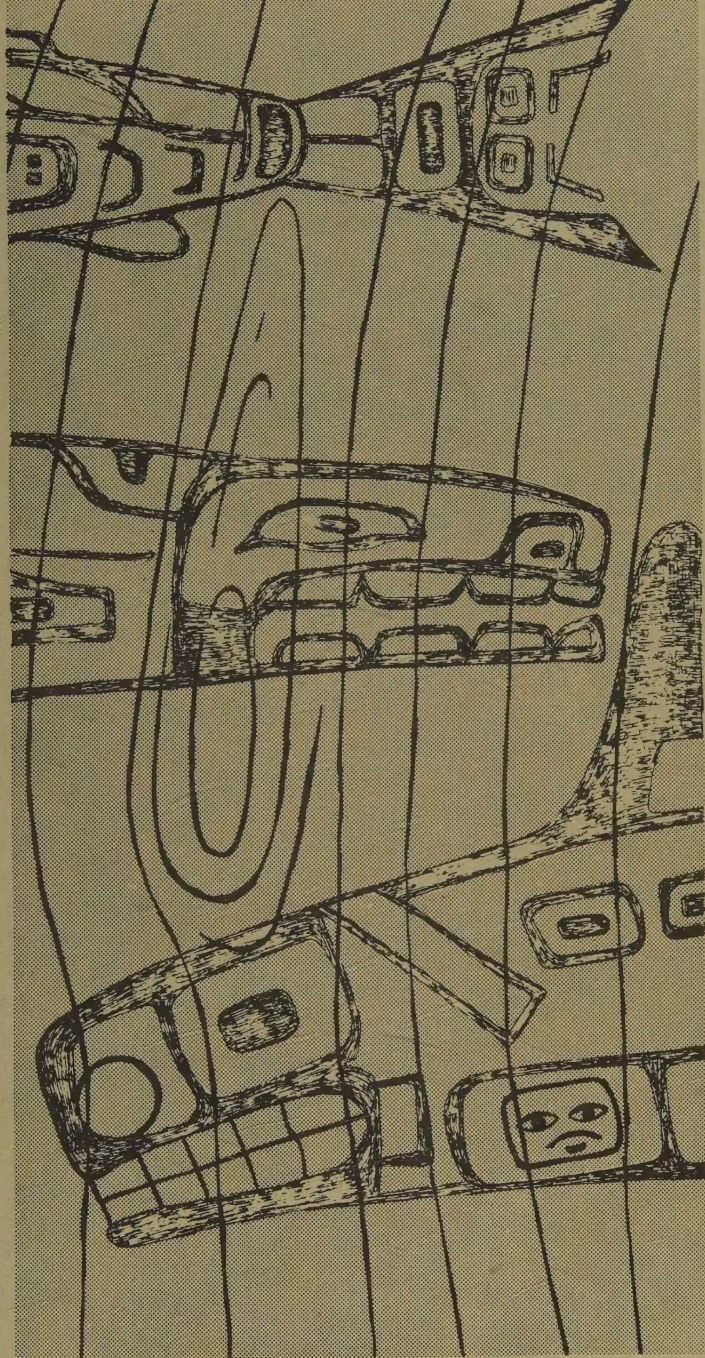


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U.S. FISH AND WILDLIFE SERVICE

BUREAU OF COMMERCIAL FISHERIES

FISHERY BULLETIN



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As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

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MODELS OF OCEANIC MIGRATIONS OF PACIFIC SALMON AND COMMENTS ON GUIDANCE MECHANISMS¹

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ABSTRACT

The general oceanic distribution and migratory behavior of Pacific salmon are summarized, and a model of the entire migration is developed for each of three typical stocks. The pink salmon of southeastern Alaska and British Columbia circle the Gulf of Alaska counterclockwise within an area generally bounded on the west by long. 155° W. and on the south by lat. 41° N. They travel generally "downstream" in the Alaskan Gyre and the associated currents. The pink salmon of the Karaginski district on East Kamchatka also apparently make a counterclockwise circuit of the Bering Sea and North Pacific Ocean in an area bounded approximately on the west by long. 155° E., on the south by lat. 40° N., on the east by long. 150° W., and on the north by lat. 60° N. Their migratory circuit is generally "downstream": southward in the East Kamchatka Current, eastward in the Subarctic Current, and finally westward and northward in the Alaskan Stream and the Bering Sea Gyre. The sockeye salmon of Bristol Bay make two or three counterclockwise circuits in the Bering Sea and North Pacific Ocean within an area bounded approximately on the north by lat. 60° N., on the west by long. 165° E., on the south by lat. 45°

N., and on the east by long. 140° W. The number of circuits depends upon the number of winters spent by the salmon at sea. In general, they travel "downstream" in the major current systems within the area defined. The time schedule, rate of travel, and average size of the fish at various stages are described for each of the three stocks.

On the basis of this summary, we believe that the salmon's migrations could not be performed if they migrated or drifted at random, or if they depended on memorized visual or olfactory cues except for final location of the home estuary and stream. The salmon predominantly travel actively with the residual ocean currents in circular migration routes. Many races could accomplish their migrations by moving down or across currents until close to the mouths of their home streams, where they might recall memorized olfactory cues. Also, ocean currents produce electric potentials in a range that some fish can detect; therefore, salmon might depend for navigation on electromagnetic cues from ocean currents. Furthermore, their responses to all migratory cues must be inherited, not memorized.

The return of the salmon to its home stream, to the part of the stream where its parents spawned, or even to the hatchery where it was reared as a fry has been well documented. Clearly, it is a most unusual animal migration. Not only does the salmon return to its birthplace to spawn and die, but each successive generation appears along the coast, enters the estuary, and ascends to the spawning grounds within a few days of the same schedule.

The appearance of the salmon in coastal waters and its final ascent of the stream are only the last acts in a most remarkable series of migrations that

have been studied only recently in enough detail to permit a reasonably comprehensive description. The impetus for the study developed when Canada, Japan, and the United States agreed on a convention concerning North Pacific salmon which required that the high-seas migrations of major stocks of salmon near long. 175° W. and the Aleutian Islands be learned in detail. Beginning in 1955 programs were financed to study the abundance, migration, and habits of the salmon in the central North Pacific and the Bering Sea and to learn much more about their environment. These studies have expanded to include the range of the salmon on both sides of the North Pacific, so that

¹ Contribution No. 269, College of Fisheries, University of Washington.

now there are available reasonably complete data on the abundance and distribution of the salmon and on their North Pacific environment (Hartt, 1962; Ridgway, Klontz, and Matsumoto, 1962; Fukuhara, Murai, LaLanne, and Sribhibhadh, 1962; Callaway, 1963; Dodimead, Favorite, and Hirano, 1963; Mosher, 1963; Favorite and Hanavan, 1963; Amos, Anas, and Pearson, 1963; Margolis, 1963; Kasahara, 1963; Manzer, Ishida, Peterson, and Hanavan, 1965; Godfrey, 1965; Mason, 1965; Tanaka, 1965; Kondo, Hirano, Nakayama, and Miyake, 1965; Hartt, 1966).

The abundance and distribution of salmon at sea are dynamic and variable. The salmon occupy almost all of the North Pacific Ocean north of about lat. 41° N. in the winter or lat. 48° N. in the summer and all of the Bering Sea south of the ice pack. They are found mostly in the upper 10 m.—far from any contact with the bottom. The maturing individuals, which are due in their spawning streams sometime between June and December, begin to move rapidly 1 to 2 months before their arrival dates and commonly maintain average speeds of 30 miles (55 km.) per day² for many hundreds of miles. Major numbers of several groups of salmon may, thus, pass through a particular ocean area within 3 weeks. The immature salmon, which remain in the ocean at least another year, commonly undertake extensive feeding migrations generally in a counterclockwise circular pattern that is repeated annually. The salmon of the different species are usually mixed. The mature and immature salmon of one species are sometimes mixed and sometimes segregated. The different stocks of a single species commonly vary as much in their distribution as do the different species, although in the early spring sockeye salmon (*Oncorhynchus nerka*) tend to predominate at the northern boundary of salmon waters and pink salmon (*O. gorbuscha*) at the southern.

The information on ocean migrations is as yet only fragmentary, partly because of the difficulties and expense of working in the autumn and winter and partly because of the lack of suitable gear and techniques for the study of the distribution and migrations of the young salmon after they have left the estuary. We do have enough information, however, on some important stocks to describe their

migrations in considerable detail and to make some inferences to fill the gaps in our information. We shall undertake, therefore, to construct models of the ocean migrations of three typical stocks originating in diverse geographical areas: southeastern Alaska and central British Columbia pink salmon; East Kamchatka pink salmon; and Bristol Bay sockeye salmon. Substantial information is available on these stocks, and all three are large enough to have been identifiable in the ocean with reasonable certainty. Fragmentary data on other stocks and species agree with these in principle. The models will illustrate the features of the migration, the navigational problems of which we are now aware, and the kinds of position- and direction-finding information that we presume are available to the salmon.

Our discussion rejects or extends and complements the summaries and hypotheses about high-seas migrations that some authors have set forth recently. We reject the general applicability of the hypothesis about random movement of salmon suggested by Saila and Shappy (1963). We extend the hypotheses about electric navigation presented by Waterman (1959). We extend with new information the thorough review of the oceanic migrations of Pacific salmon by Neave (1964). We question and limit the applicability of sun-compass and odor-perception mechanisms hypothesized by Hasler (1966); Hasler, Horrall, Wisby, and Braemer (1958); and Hasler and Schwassmann (1960).

Perhaps our information concerning salmon migration will help to explain the mechanisms used by other aquatic species that undertake long-range oceanic migrations and about which much less is known. In the Pacific these fishes now include the albacore (*Thunnus alalunga*), skipjack tuna (*Katsuwonus pelamis*), bluefin tuna (*Thunnus salsiens*), black cod (*Anoplopoma fimbria*), and dogfish (*Squalus acanthias*); numerous species of marine mammals and turtles also are known to migrate extensively at sea.

The migrations of the salmon begin when the fry emerges from the gravel. These first few inches of migration through the gravel may well be the most hazardous of its entire life. It then moves downstream (or occasionally upstream) to sheltered waters. Coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) usually find shelter and food in rivers and streams; sockeye salmon in

² The miles used throughout this paper are nautical miles.

lakes; chum salmon (*O. keta*) and pink salmon in salt-water estuaries and bays. The physiological change from fresh water to salt water is highly significant, but the ecological change is not. The young salmon needs a place with food and protection from its enemies, and this it finds along the shores of lake, river, or estuary. After it reaches a length of about 5 to 8 cm. it may move to bigger waters where the feeding is better, and at a size of 10 to 15 cm. it usually seeks the open sea. This is where our story of the ocean migrations begins.

OCEAN MIGRATIONS OF PINK SALMON OF SOUTHEASTERN ALASKA AND BRITISH COLUMBIA

Of the Pacific salmon, pink salmon probably have the least complicated oceanic migrations because of their short and uniform 2-year life history. The pink salmon stocks about which we have the most comprehensive knowledge of migrations are those of southeastern Alaska and British Columbia originating between Cape Flattery, Wash. (lat. 48° N.), and Cape Spencer, Alaska (lat. 58° N.)—figure 1. Washington State pink salmon form part of these stocks in odd-numbered

estuaries and bays for 2 or 3 months. As they attain a size of 5 to 6 cm., they venture farther offshore.³ They migrate to the ocean proper in July, August, and September, at a length of 12 to 15 cm. (Gillhouse, 1962; Neave, 1966; Hartt, Dell, and Mathews, 1966).

The ocean migratory period of these stocks, typical of that of pink salmon, extends approximately from July of the year after spawning until summer or early autumn of the next year. On the basis of recent research, we can now describe or hypothesize within moderate limits of dependability the migrations of the southeastern Alaska and British Columbia pink salmon throughout essentially all stages of their 12 to 14 months at sea.

SUMMER EMBARKATION

Juvenile pink salmon enter the ocean proper at numerous points along the southeastern Alaska-British Columbia coast during July, August, and September; their abundance apparently peaks in August (Martin, see footnote 3; Hartt et al., 1966). They do not scatter randomly seaward, but turn northward and migrate along the coast in a narrow band extending about 20 miles (37 km.) offshore (Hartt et al., 1966). They continue in this manner around the northern periphery of the Gulf of Alaska and southwestward past Kodiak Island. The band widens, in the northern part of the Gulf, presumably because there the Continental Shelf is wider. Stocks other than those from southeastern Alaska and British Columbia undoubtedly join the procession off Prince William Sound, Cook Inlet, and Kodiak Island (Hartt, Smith, and Dell, 1967).

The width of the band and the northerly direction of migration were determined by fishing a large, fine-meshed purse seine at various distances from shore and by facing the net in opposed directions. The seine was set in a semicircle, held open for 30 minutes, and then closed to collect fish migrating toward the opening of the seine. Catches were large when the seine was held open to the southeast and small when open northwest (Hartt et al., 1966). For example, in 1964 off southeastern Alaska, the average catch was 350 fingerlings when

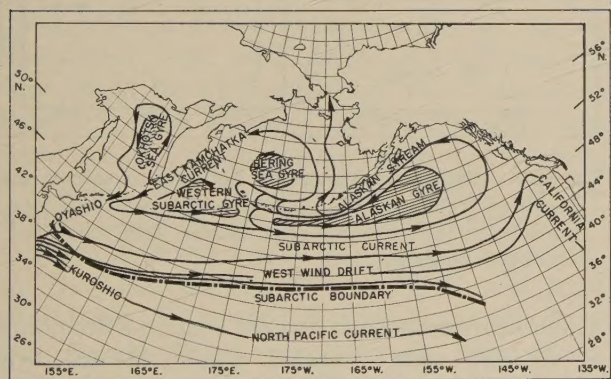


FIGURE 1.—Base map of North Pacific area and surface circulation (adapted from Dodimead et al., 1963, fig. 109).

years. Spawning takes place from mid-July to mid-October, but tends to be earlier in the more northerly areas. Fry emerge from the gravel from February through June; the peak period is in April and May (Sheridan, 1962; Neave, 1966). The fry immediately migrate downstream to salt water and then feed in schools along the shores of

³ Martin, John W. 1964. Studies of estuarine and inshore marine ecology of juvenile pink salmon in southeastern Alaska. In W. J. McNeill (editor), Report of the 1964 northeast Pacific pink salmon workshop and contributed papers. U.S. Fish Wildl. Serv., Bur. Comm. Fish., Biol. Lab., Auke Bay, Alaska, Manuscript Rep. 64-5: 80-83.

the seine was open southeast and zero when it was open northwest.⁴ A time-space extrapolation of the average catch (in 30 minutes in a ¼-mile-wide [0.46-km.] band) indicated that at least 750,000 juveniles migrated daily past any given line of latitude off southeastern Alaska in 1964. Thus, for the 30 to 60 days of strong migration, it is evident that major stocks of fish were involved.

The fork length of the pink salmon at this stage varies from 10 to 25 cm. The average size was significantly larger in the northern samples, presumably because of the presence of fish which had already migrated a considerable distance from southern production areas (fig. 2). The northern samples also included small fish that presumably had just entered the sea from nearby channels and bays. Mixed with the juvenile pink salmon were juvenile sockeye, chum, coho, and chinook salmon and steelhead trout (*Salmo gairdneri*), which suggests that the migratory cue at this stage is similar for all species.

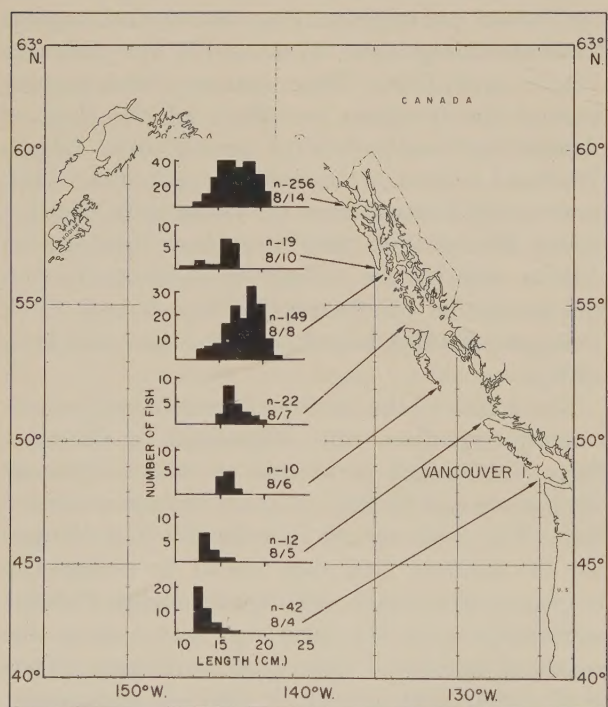


FIGURE 2.—Fork lengths of juvenile pink salmon sampled August 4–14, 1964, in eastern Gulf of Alaska.

⁴ For a discussion of the validity of purse seine gear for determining directional migrations of salmon in areas of strong ocean currents, see Hartt (1966 : 8–10).

The northward migration of juvenile salmon is indicated by the purse-seine catches and tag returns. Six pink salmon were recovered a year after tagging, all in southeastern Alaska (fig. 3). All were recovered south of the point of release. If it is assumed that they entered the ocean near the point where they were recaptured as maturing fish, they must have migrated northwestward before they were tagged. The specimen tagged near lat. 59° N. by long. 138° W. had traveled about 350 miles (648 km.) by September 22, 1961, when it was tagged. Figure 3 also illustrates the locations of release and recovery for 1 sockeye salmon, 1 steelhead trout, and 58 coho salmon that were tagged as juveniles, along with the pink salmon.

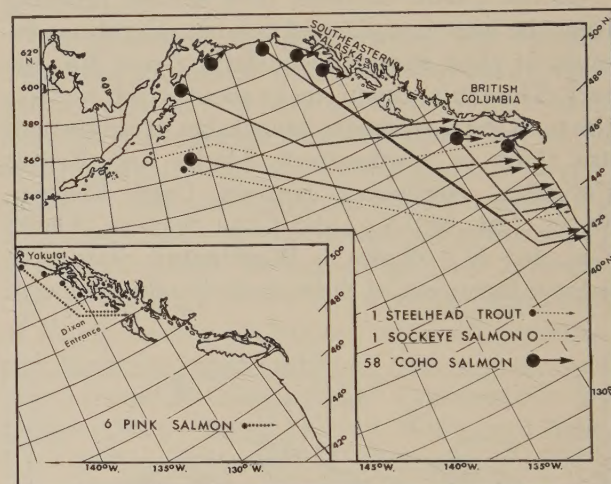


FIGURE 3.—Release and recovery diagram of salmon and steelhead trout tagged as juveniles and recovered 1 or 2 years later (all coho and pink salmon were recovered 1 year after tagging).

These fish were also recovered south of the points of release; some traveled northwestward over 1,000 miles (1,852 km.) before they were tagged.

The rate of travel of juvenile pink salmon during their first few months at sea is difficult to estimate on the basis of the few tag returns received to date, because the distances involved are relatively short and the date of ocean embarkation can only be approximated. If we assumed that the specimen tagged near Yakutat (fig. 3) on September 22 had left Dixon Entrance on August 1, and then had followed the coastline (350 miles or 648 km.), its rate of travel would be 6.6 miles (12.2 km.) per day. By the same method, if we as-

sumed that the sockeye and coho salmon and the steelhead tagged south of Kodiak Island had embarked as juveniles on May 1, then they each covered about 1,400 miles (2,593 km.), in about 4 months preceding tagging, at an average rate of 11.6 miles (21.5 km.) per day. The May 1 embarkation date is probably correct for the steelhead trout; it was fin-clipped and released in the Alsea River, Oregon, sometime in April 1958. The estimated rates of travel of the latter three juveniles are probably more accurate than the estimated rate of travel of the single pink salmon, so that 10 miles (18.5 km.) per day might be a good working estimate of rate of travel during the initial stage of their ocean migrations.

AUTUMN AND WINTER MIGRATIONS

We have much less data on the autumn and winter migrations, but the general pattern can be deduced from the substantial data on the location of juveniles in late summer and of maturing fish in early spring. By late September, most pink salmon have entered the sea, but substantial numbers still are along the coast from southeastern Alaska to Kodiak Island; juvenile migration must continue, therefore, into October and November. Neave (1964) reported 163 juvenile pink salmon in a trawl catch in Dixon Entrance (lat. 54° N.) on November 5, 1963. After the end of September, the next period for which there are data is January–February, when longlines and gill nets have been fished in recent years, although somewhat sparsely, throughout much of the Gulf of Alaska.⁵ Results in 1964 indicated few, if any, pink salmon in the northern Gulf but a wide dispersion in the southern Gulf between lat. 45° and 51° N. and from about long. 133° to 156° W. (fig. 4). At this stage they average 30 cm. long (French, 1966; International North Pacific Fisheries Commission, Annual Report, 1964: 30).

Thus, between midautumn and midwinter, the young pink salmon must leave the coastal belt along the northern Gulf and migrate well to the south, where they are scattered widely in the open sea. The points at which they leave the coastal belt are unknown. They probably do not follow the Alaskan Stream very far to the west, however,

⁵ For convenience, *Gulf of Alaska* as used herein refers to all salmon waters east of long. 165° W., thus extending to about lat. 40° N., in conformance with the general oceanic regions described by Manzer et al. (1965).

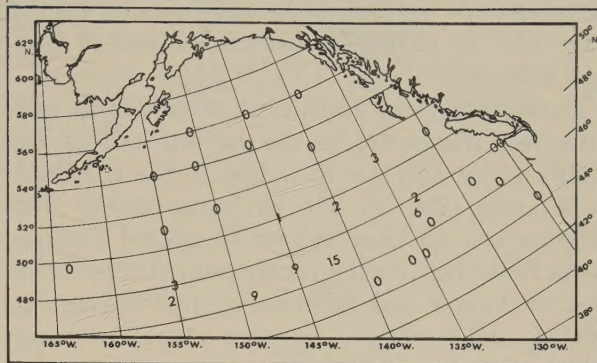


FIGURE 4.—Catch of pink salmon per longline set during winter of 1964. Canadian and United States operations January 7 to February 9 (30 sets, each using 5 to 35 skates—one skate=49 hooks).

because immature pink salmon have never been taken in the extensive seining in the summer and autumn south of the eastern Aleutian Islands. Furthermore, extensive tagging of mature pink salmon in spring and summer south of the Aleutians has yielded returns only from East Kamchatka and western Alaska; none were returned from southeastern Alaska or British Columbia nor from any other Gulf coastal areas. Thus, the stocks in question probably leave the coastal belt east of long. 160° W. Such a southward migration would place them in the eastward-flowing Subarctic Current, on a counterclockwise route back toward their embarkation points (fig. 1). The distance from the northern Gulf to the center of their winter distribution is at least 1,000 miles (1,852 km.), which, if covered in 90 days, would indicate a minimum rate of travel of 10 miles (18.5 km.) per day.

SPRING-SUMMER HOMING MIGRATIONS

The ocean migrations of the maturing pink salmon during their last spring and summer at sea are well documented by a number of years of longline and purse seine sampling throughout the Gulf from late March through mid-August (Neave, 1964; International North Pacific Fisheries Commission Annual Reports, 1961–65). In April pink salmon of the southeastern Alaska-British Columbia stocks are located mainly in the southeastern part of the Gulf east of long. 150° W. and between lat. 43° and 50° N. and are mixed with stocks from Prince William Sound, Kodiak Island, Cook Inlet, and the Alaska Peninsula. The British Colum-

bia stocks are farthest to the east—mainly east of long. 135° E. (Fisheries Research Board of Canada, 1962–66).

During May and June, pink salmon shift progressively northward in the eastern half of the Gulf and by July are abundant in the northernmost areas (fig. 5). The early-run stocks then migrate toward their respective coastal destinations. Later-run fish frequently return to the southeast in August and September after having migrated northward past their area of origin (Neave, 1964). For these fish the late-season homing migration follows in reverse the coastwise route taken by the juveniles in the Alaskan Gyre and is “upstream” instead of “downstream.” Returns of tagged fish to southeastern Alaska and British Columbia in 1962 (fig. 6) illustrate the spring-summer distribution and migrations of these stocks.

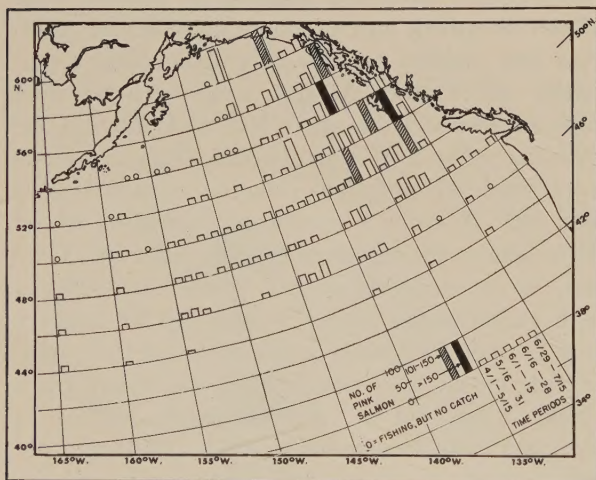


FIGURE 5.—Average catch of pink salmon per 20 skates of longline gear (49 hooks per skate) by area and by time period in 1966 (U.S. and Canadian data unpublished).

The rate of movement of the center of abundance from mid-April to mid-June appears to be about 7 miles (13 km.) per day (if movement is estimated from lat. 48° to 55° N. during the 60-day period). Rates of travel of individual tagged fish based on straight-line distances to recovery points vary from 5 to over 40 miles (9.3–74.1 km.) per day. Mean fork lengths at this stage vary from 45 to 55 cm., or even larger for late-season spawners.

The final migrations through channels and bays to the natal streams need not be reviewed in this paper except to note that coastal tagging indicates considerable “searching” or “to and fro” migrations as the numerous stocks approach their home estuaries (Noerenberg, 1959; Verhoeven, 1952).

SUMMARY

The oceanic migration of southeastern Alaska-British Columbia pink salmon is shown diagrammatically in figure 7 according to four time periods. The western limits and the southern limits are only approximate. After spending 3 to 5 months in estuaries and inner bays and channels, juvenile pink salmon enter the ocean proper in July to September at a length of 10 to 15 cm. They travel rapidly northward and westward along the coast, following the Alaskan Gyre. By late September and early October they average 20 to 22 cm. long. Their average rate of travel is about 10 to 12 miles (18.5–22.2 km.) per day. Between October and midwinter they migrate southward and in January to February are spread widely between lat. 41° and 51° N. and from long. 130° to 160° W. and have continued to migrate at least 10 miles (18.5 km.) per day. At this stage the mean length is 30 cm. In their final spring and summer, they migrate northward in the eastern Gulf from April through July, then coastward to their respective destinations; the late-spawning stocks turn back southeastward to return to their areas of origin. Mean sizes at maturity vary from 45 to 55 cm. Rates of travel in final coastward migrations are at least 10 miles (18.5 km.) per day; some individuals migrate over 45 miles (83.3 km.) per day.

OCEAN MIGRATIONS OF PINK SALMON OF EAST KAMCHATKA

Although data are fewer on the ocean migrations of East Kamchatkan pink salmon than for the southeastern Alaska-British Columbia stocks, the probable sequence of migration can be inferred and certain similarities and contrasts indicated.

The East Kamchatkan stocks (mainly the Karaginski district, fig. 8) are substantial, over 40 million adults in some odd-numbered years.⁶ The spawning migration in the Karaginski region is

⁶ From: “Pacific salmon catch statistics of the Union of Soviet Socialist Republics 1940–1958” (plus similar tables for individual years 1959–64), as given to the International North Pacific Fisheries Commission by the All-Union Research Institute of Marine Fisheries and Oceanography, Moscow, unpublished.

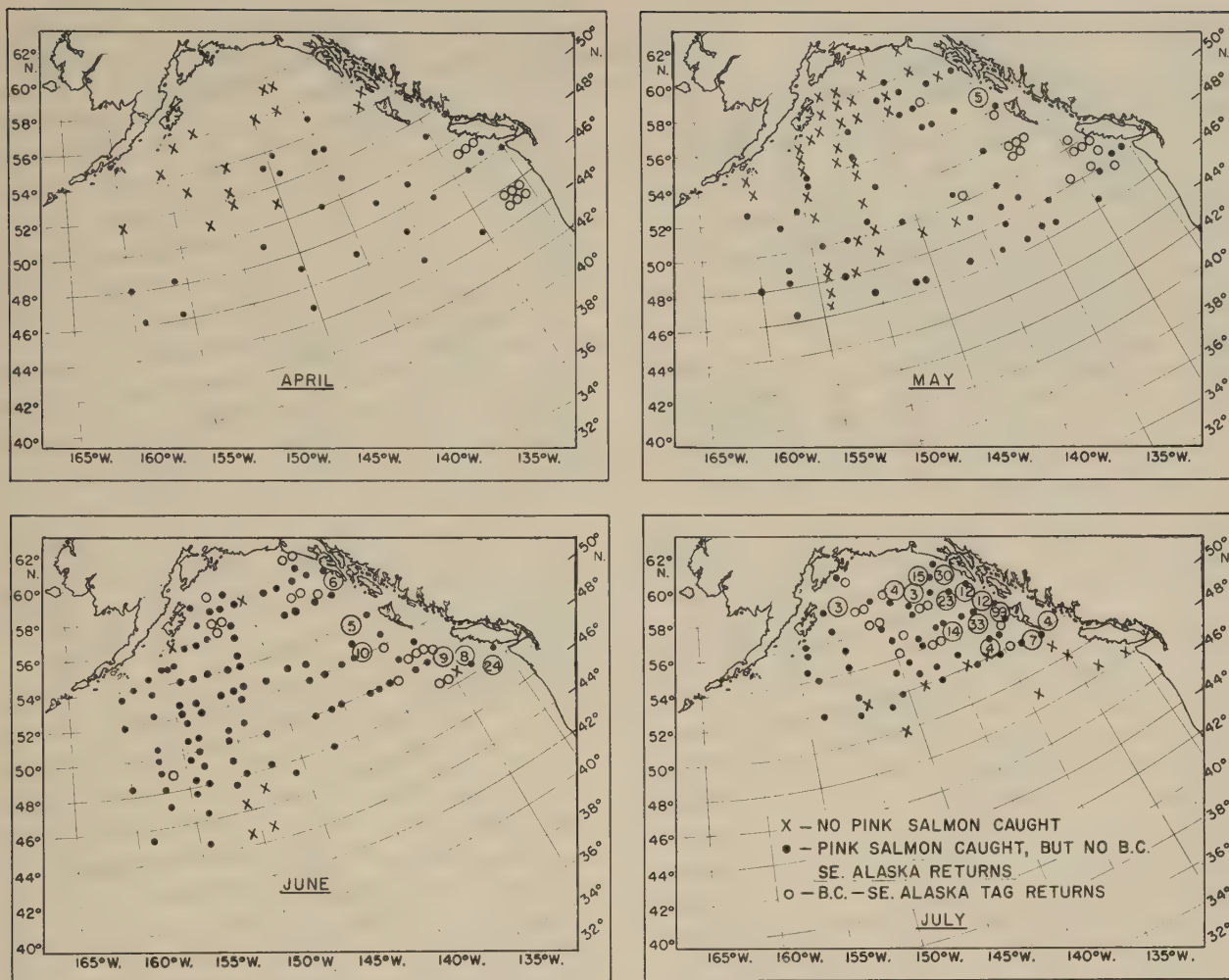


FIGURE 6.—Spring-summer distribution of southeastern Alaska-British Columbia pink salmon in the Gulf of Alaska in 1962 as shown by longline and purse seine catches and by tag returns (source: Canadian and U.S. data, International North Pacific Fisheries Commission Annual Report, 1962).

relatively brief and occurs principally in July (Kaganovskii, 1949). The fry probably migrate to sea in June, but data are lacking.

If the East Kamchatkan pink salmon respond to ocean currents as do the southeastern Alaska-British Columbia stocks, then they may be expected to follow the East Kamchatka Current southwestward along the coast and then to migrate eastward with the Subarctic Current and the West-wind Drift (fig. 1). Their presence in the western Gulf of Alaska (near lat. 50° N. and long. 155° to 160° W.) in May and June has been demonstrated by tag returns (Fisheries Research Board of Canada, 1963; Hartt and Dell, 1964). Their presence south of the entire Aleutian chain from late May

through early July and in the Bering Sea in June and July has also been well demonstrated by Japanese and United States tagging (Hartt, 1962; Kondo et al., 1965). Purse seining by the United States has further shown that they move very rapidly in a westward direction south of the Aleutian Islands, northward through the major passes, and northwestward in the Bering Sea. Passage south of the central Aleutians peaks sharply about June 5 to 30.

The rate of travel to the Karaginski district from the central Aleutians (about 800 miles or 1,482 km.) averages about 25 to 30 miles (46.3–55.6 km.) per day for the last 30 to 45 days at sea (Hartt, 1966). Thus, the migration is more

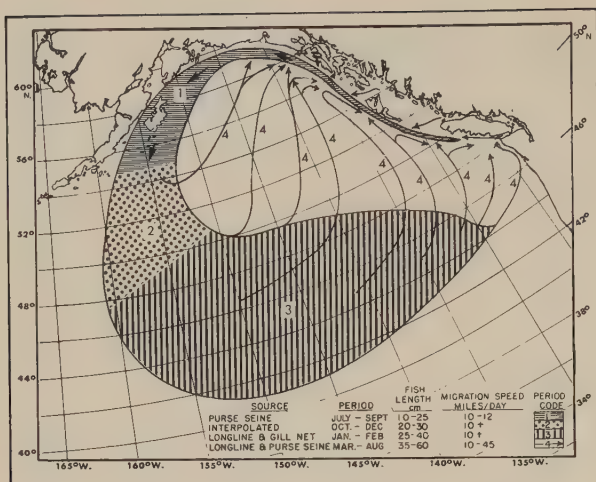


FIGURE 7.—Diagram of ocean migrations of pink salmon stocks originating in southeastern Alaska and British Columbia.

directed and rapid than that of the southeastern Alaska-British Columbia pink salmon, perhaps because the East Kamchatka stocks have a more limited time of arrival.

Recoveries of tagged pink salmon at sea suggest that the fish migrate rather directly toward their coastal destination from the point of release (fig. 8). Ishida (1960) suggested that the fish apparently follow parallel courses toward the Karagin-ski district from whatever point they enter the Bering Sea. Such an ability to navigate toward "home" is in agreement with Neave's thesis (1964) that to perform the observed migrations salmon at sea must maintain "bico-ordinate orientation" (i.e., oriented with respect to "home" in two components such as east-west and north-south).

The postulated migration of East Kamchatka pink salmon is diagrammed in figure 9. The first two steps—migration downstream in the East Kamchatka Current and in the Subarctic Current and Westwind Drift—are assumed (figs. 1 and 9). Direction appears to change abruptly as they depart the eastward-flowing Subarctic Current and join the westward-flowing Alaskan Stream. The influence of the Bering Sea Gyre on the migration route is unknown, but the tagging data illustrated in figure 8 indicate that migration continues rather directly through the Gyre.

A significant feature of the migration of the Karagin-ski pink salmon is that throughout much of their route during their last 60 to 90 days at sea

they are intermingled little with other pink salmon stocks although they are extensively intermingled with sockeye and chum salmon. In the western part of their distribution they are mixed with West Kamchatka and other Sea of Okhotsk stocks, and in the eastern extreme they mix with Gulf of Alaska stocks (Hartt, 1966). In the central part of their oceanic range they are mixed only with the relatively minor Aleutian and western Alaska stocks. Tagging data indicate that their distribution is probably just as extensive in even-numbered years of low abundance as in odd-numbered years of high abundance. In addition, the abundant West Kamchatka or Gulf of Alaska stocks do not move into the central Aleutian area in years when the East Kamchatka stocks are scarce (Hartt, 1966; Kondo et al., 1965). These observations indicate that oceanic-migration patterns are independent of abundance within or between individual stocks.

OCEAN MIGRATIONS OF SOCKEYE SALMON OF BRISTOL BAY

Bristol Bay stocks are defined herein as those originating in the eastern Bering Sea between the northern side of Unimak Island and the Kuskokwim River (fig. 10); fish originating within this area migrate similarly at sea. Nearly all originate in five main river systems—Nushagak, Kvichak, Naknek, Egegik, and Ugashik—which enter at the head of Bristol Bay near lat. 58° N., long. 157° W. (fig. 10). These stocks make up the largest sockeye salmon run in the world, between 6 and 60 million mature fish per year. The annual average for 1956–65 was 23.9 million (Ossiander, 1965; Pacific Fisherman, 1966).

The life history of Bristol Bay sockeye salmon, although variable, may be described in general as follows. Spawning takes place in August and September in the vast Bristol Bay lake systems. Fry emerge mainly in June. The young fish generally spend 1 or 2 winters in fresh water and migrate to sea as 2- or 3-year-old smolts. Downstream migration is mainly in June, simultaneously with or immediately after breakup of the lake ice. Most then spend 2 or 3 years at sea so that their total age at maturity is usually 4, 5, or 6 years with various combinations of fresh-water and salt-water age. The returning run migrates through the estuaries from about June 20 through July 25, but

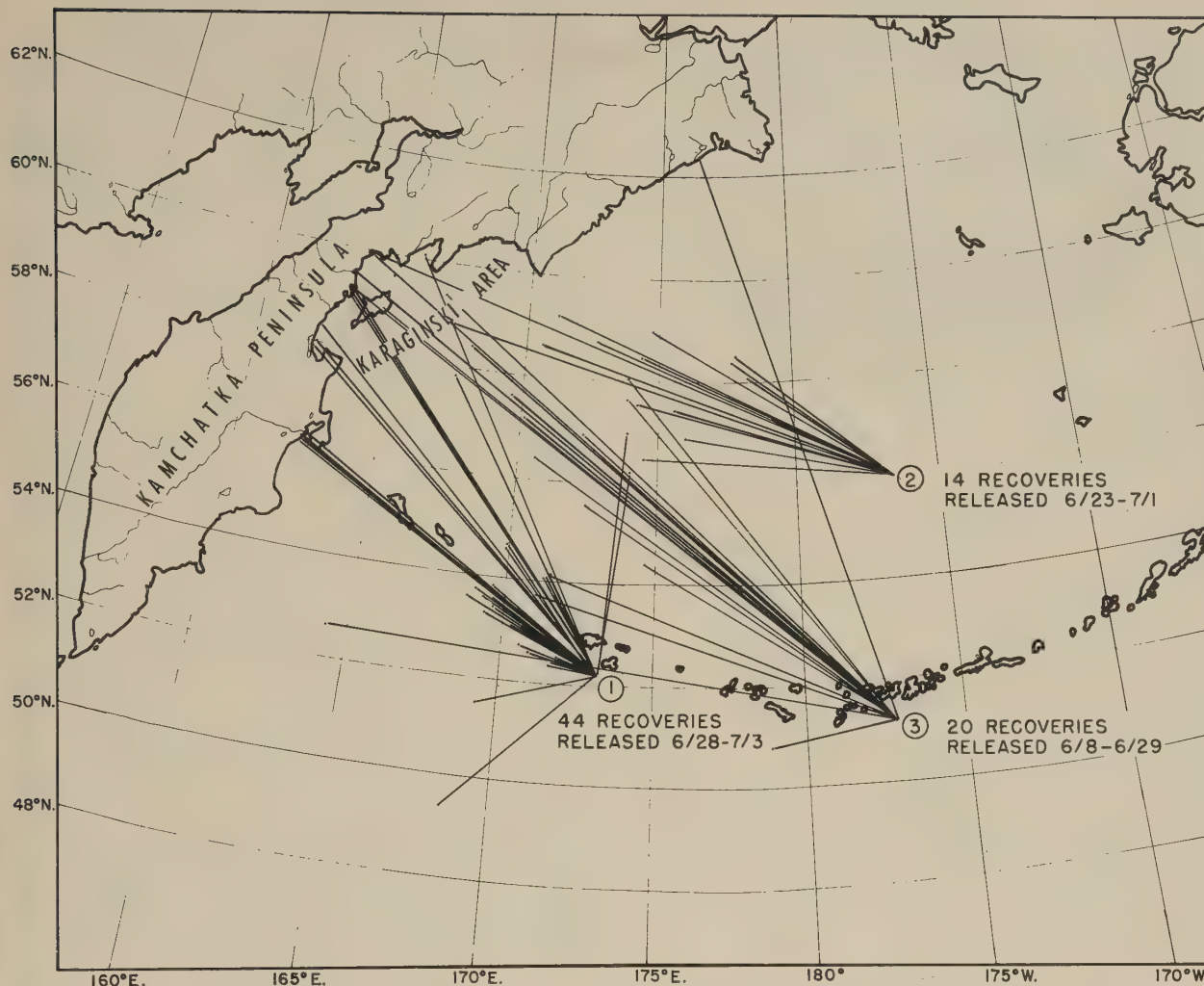


FIGURE 8.—High-seas and coastal recoveries of pink salmon tagged at three points in the North Pacific Ocean and Bering Sea in 1959.

over 80 percent of the run arrives within 9 to 22 days, and this arrival period occurs regularly between June 23 and July 18 (Royce, 1965). The peaks of the run vary only from July 2 to July 9.

The ocean migrations of the Bristol Bay sockeye salmon have been studied intensively more than 10 years (International North Pacific Fisheries Commission, 1957-66). Excellent data are available for the spring and summer periods, and some winter data are available, so that the entire migratory pattern can be inferred.

FIRST YEAR AT SEA

The smolts from the five main river systems enter the coastal waters of Bristol Bay in an intensive mass migration that peaks sharply during

June. Their length at this stage typically ranges from 7 to 12 cm., varying according to river system and fresh-water age. During July, they travel at least as far westward as long. 164° W. (250 miles [463 km.] from the Naknek-Kvichak estuary) and are apparently most abundant near the Alaskan Peninsula. Observations at this stage are based on limited purse seining in 1962 and 1966 (unpublished). Purse seine catches ranged up to 1,300 fish per set. At this stage they feed heavily on euphausiids and larval fish and grow rapidly; the average size of those in the westernmost samples ranged from 13 to 15 cm. in July.

After this early marine stage, data on their migrations are few until they appear a year later

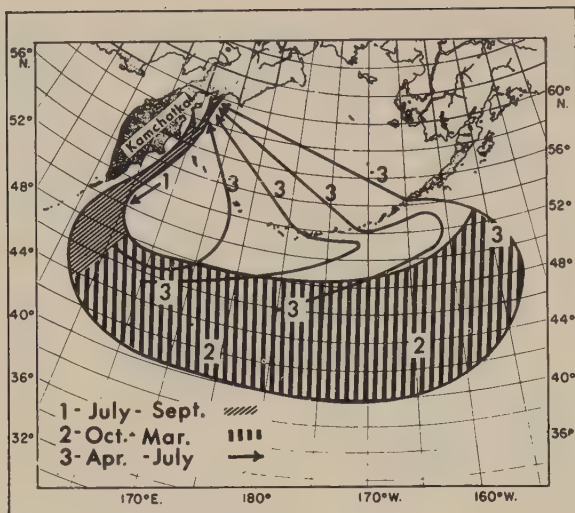


FIGURE 9.—Diagram of probable ocean migrations of pink salmon stocks originating in East Kamchatka.

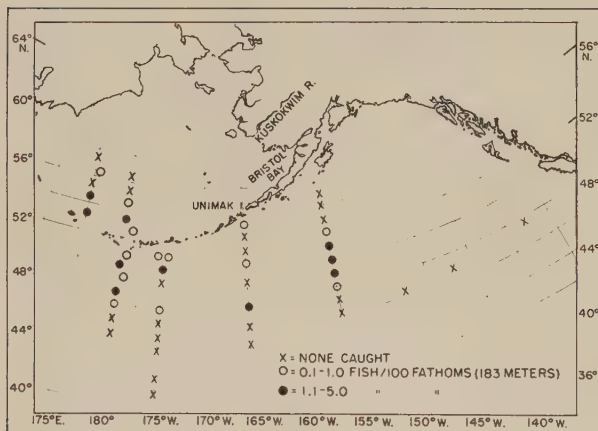


FIGURE 10.—Catches of .1-age sockeye salmon during winter gill netting in 1962 and 1963 (source: French and Mason, 1964).

as .1-age⁷ immature fish of 35-cm. average length migrating westward in large numbers along the south side of the Aleutian Islands. Two items of indirect evidence, however, help fill in the first year's migration. First, the Bristol Bay sockeye salmon apparently do not migrate south of the Aleutians during their first summer; .0-age juveniles were extremely rare in the intensive purse

⁷ Ocean age designation throughout this paper is that proposed by Koo (1962) in which the number of ocean winter annuli on the scale is preceded by a decimal point (e.g., .1-age—one winter at sea).

seine sampling along the south side of the Aleutians during the summers of 1956-65 (International North Pacific Fisheries Commission, 1957-66). Second, winter sampling with gill nets (French and Mason, 1964) has shown the presence of .1-age sockeye salmon north of the western Aleutians and south of the central Aleutians during January and February (fig. 10). At this stage they average about 25 to 30 cm. long. It has not been proved that these are Bristol Bay fish, but it seems safe so to assume, because of their abundance and because tagging and other studies have shown that Bristol Bay stocks predominate in these areas in spring and summer. Thus, we may postulate that the fingerlings remain in the Bering Sea at least until autumn, and their winter distribution suggests that they reach the western Bering Sea and proceed southward into the North Pacific. The next move must be eastward in the Subarctic Current to place them in position by late spring to make the characteristic summer migration westward with the Alaskan Stream along the south side of the Aleutian Islands—a migration which has been extensively studied and described (Hartt, 1966). The postulated first year's migration is diagrammed in figure 11A as part of the schematic of their entire ocean travels. The first year's migration could be accomplished at an average rate of 10 miles (18.5 km.) per day, which is the rate indicated for the juveniles tagged near Kodiak Island in the Gulf of Alaska discussed earlier.

SECOND YEAR AT SEA

During their second summer at sea, Bristol Bay sockeye salmon are immature .1-age fish averaging 35 cm. long. They migrate westward south of the Aleutian Islands in a more or less continuous band, from late June through mid-September. The band extends offshore about 100 miles (185 km.), but the greatest abundance is usually within 30 miles (55.6 km.) (French, 1964; Hartt, 1966). The fish apparently approach from areas to the south and east and continue far westward and north-westward, as shown by tag returns from the high-seas fleet in the year of release (fig. 12). The dominance of Bristol Bay stocks is demonstrated by coastal tag returns 1 year later (fig. 12) and by the relation between age composition and abundance at sea and age composition and abundance in the Bristol Bay run 1 year later (Ossiander, 1965). Some idea of the magnitude of the

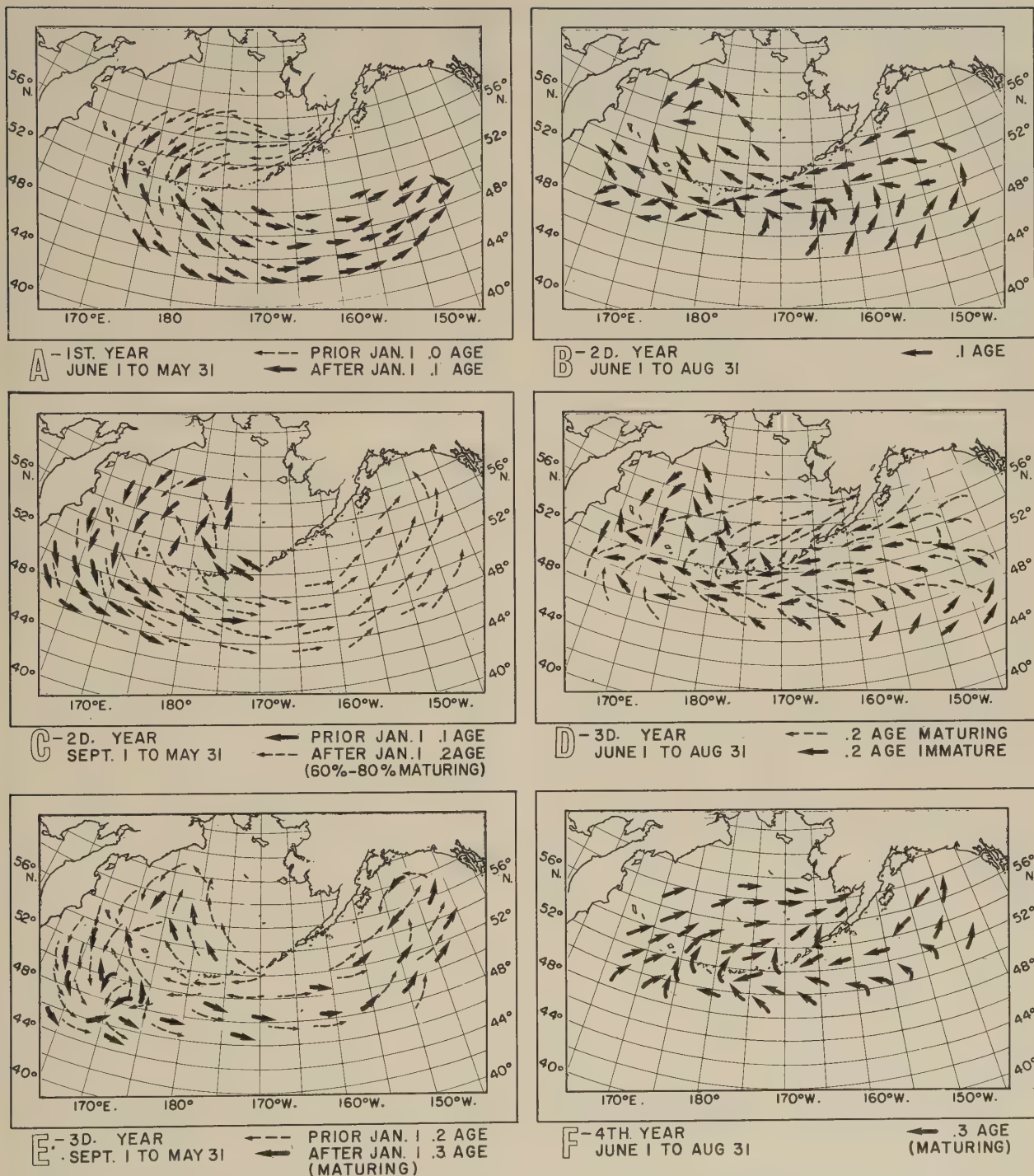


FIGURE 11.—Diagram of ocean migrations of Bristol Bay sockeye salmon based on seine catch and tagging data through 1966; arrows indicate direction and approximate distribution.

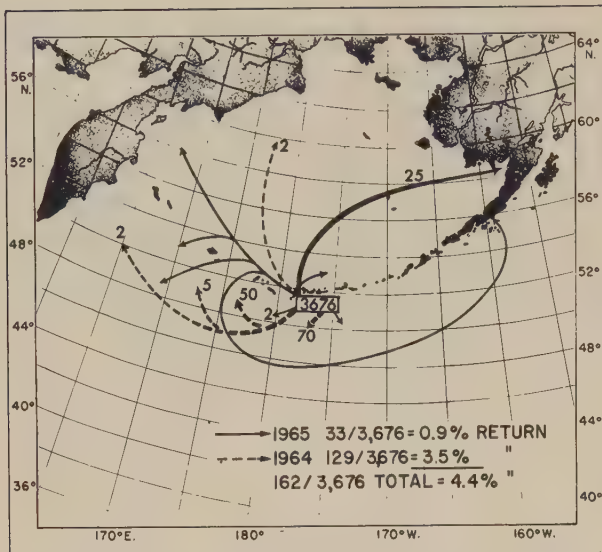


FIGURE 12.—Recovery distribution of sockeye salmon tagged as .1-age immature fish at Adak in 1964 (the arrows depicting returns in 1965 are merely drawn for convenience and are not intended to show migrations during the full year at liberty).

numbers can be gained from a conservative time-space extrapolation of the average catch per 30-minute seine set; in 1964 a minimum of 0.5 million .1-age sockeye salmon per day passed westward south of Adak Island from late June through late August, or about 30 million of this age group alone. The rate of travel averaged 17 miles (31.5 km.) per day for those recovered by the Japanese fleet in 1964. Stomach examinations indicated that the fish feed actively on various crustaceans and larval fish (Dell, 1963). The probable summer migration of the .1-age immature fish is summarized in figure 11B.

The fact that the .1-age fish migrate past a given point for a long period indicates that they must be spread over a large area at sea. Such an extended distribution is probably characteristic of salmon in general even in their first summer, as evidenced by the long band of .0-age salmon of all species along the coast of the Gulf of Alaska described earlier. It is important to emphasize here that the .1-age immature sockeye salmon at this stage are thoroughly mixed with the .2-age immature fish that left Bristol Bay a year earlier; apparently they overtake the previous year's smolts and then follow a similar migratory path.

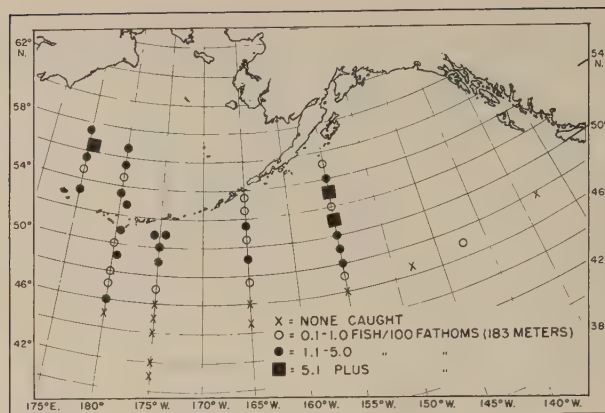


FIGURE 13.—Catches of .2-age and older sockeye salmon during winter gill netting in 1962 and 1963 (source: French and Mason, 1964).

The winter data (figs. 10 and 13) indicate that the intermingling of the age groups takes place as early as January. In general, however, the .1-age group in figure 10 was farther south than the older fish shown in figure 13. Thus, it would appear that the migration of this age group is independent of the older fish at this early stage.

The migrations during the autumn and winter of the second year at sea can be inferred from the limited winter sampling and from the distribution and migrations observed in the following spring and summer (fig. 11C). During this period the .1-age fish add another winter mark on their scales and become .2-age fish. Some will mature in this year and migrate homeward to spawn, but others will remain at sea to mature a year later at .3-age. As illustrated in figure 13, .2-age sockeye salmon are distributed widely during the winter (January–March) in the central and western Bering Sea and in the North Pacific at most sampling stations north of lat. 45° N. As at other times of the year, Bristol Bay fish may be expected to be present in most of the samples. The data then suffer a gap until the following May, when samples taken by purse seines indicate few, if any, sockeye salmon in the Alaskan Stream south of the Aleutians. In late May and early June, however, the maturing .2-age sockeye salmon begin to appear in the catches along the entire south side of the Aleutians, and they are again migrating westward in the Alaskan Stream. The evidence, thus, indicates a southward shift during late winter and early

spring and a return migration toward the east in the Subarctic Current (fig. 1). The fish apparently repeat the winter-spring-summer round of migrations of their first year at sea (fig. 11A). Further support for this hypothesis is provided by the recovery in the Shumagin Islands area in the eastern Aleutians of .2-age sockeye salmon that had been tagged as .1-age immature fish a year earlier near Adak Island (fig. 12). The 1964 data are typical of other years' results. At Adak they had been part of the westward flow of immature fish, and at Shumagin Islands they were among maturing fish that characteristically migrate westward, many of them en route to Bristol Bay (Thorsteinson and Merrell, 1964).

THIRD YEAR AT SEA

The migrations during the third year at sea must be considered separately for one group that matures and returns to spawn at the end of its second year at sea (early in its third summer at sea), and another group that remains another full year at sea. From the numbers of .2- and .3-age fish returning in successive years, about 60 to 80 percent of the .2-age group mature and spawn. The fish of the maturing group average about 51 to 53 cm. in fork length and are thoroughly mixed with the older .3-age mature salmon. They approach the eastern Aleutian Islands area from the south and southeast in late May, migrate westward with the Alaskan Stream, northward through the Aleutian passes, and then northeastward toward their respective Bristol Bay estuaries (Hartt, 1966). The recovery distribution of sockeye salmon (mostly .2-age mature fish) tagged in the Aleutian Island area in 1960 is illustrated in figure 14. Those approaching from far to the west apparently migrate rather directly toward the Bay. Recaptures by the high-seas fleet illustrate the course through the central Aleutian area. The lack of high-seas returns from releases in the eastern Aleutians (fig. 14D) indicates that this group must have turned northward and entered the Bering Sea before reaching lat. 175° W. Migration speed is rapid during the final 30 to 60 days at sea, averaging 25 to 30 miles (46.3 to 55.6 km.) per day.

Even as late as May 1, sockeye salmon from Bristol Bay are distributed over vast areas at sea extending from 1,200 miles (2,222 km.) to the west off the Kamchatka Peninsula to 1,200 miles to the

east in the central Gulf of Alaska. Figure 15 illustrates the tagging areas during the period May 1 to June 15 from which Bristol Bay recoveries were subsequently received in the year of release.

The bulk of the run passes through the Aleutian Islands area between June 1 and 20, and through the estuaries between June 23 and July 18, with the peak between July 2 and 9. Tagging has indicated a sequential correspondence between date of

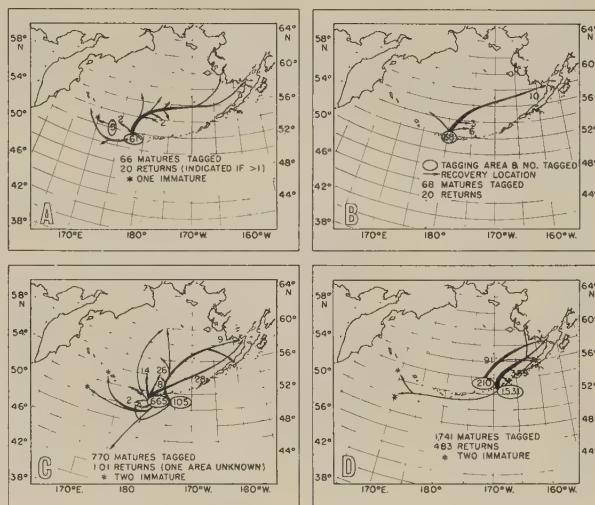


FIGURE 14.—Distribution of recoveries of sockeye salmon tagged and recovered in 1960 (U.S. tagging). Panels A, C, and D each show the results from two areas of operation; panel B shows the results from one.

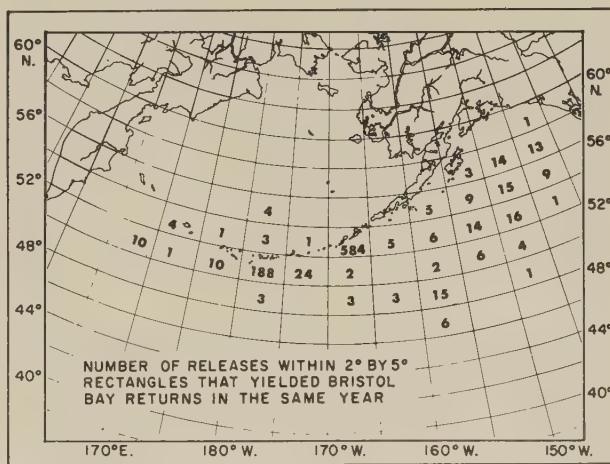


FIGURE 15.—Areas of release of sockeye salmon tagged between May 1 and June 15, and subsequently recovered in Bristol Bay in the same year between June 26 and July 24 (U.S. data 1956-65, Canadian data 1961-65, Japanese data 1958-61).

release in the Aleutians area and date of recovery in the commercial fishery and a tendency toward more rapid movement by the later migrants (Hartt, 1966). Many of the fish still feed actively on a variety of animals when within only 100 miles (185 km.) of the estuaries.

The immature .2-age fish during their third summer at sea follow a course similar to that of the .2-age mature fish except that they continue westward and northwestward in the Aleutian Islands and Bering Sea areas, rather than returning northeastward toward Bristol Bay (fig. 11D). They average 46 to 48 cm. long and are slimmer than the .2-age mature fish. Immature salmon begin to arrive in the Aleutian area just after the mature fish have passed and continue on a course similar to that described for their migrations in the previous summer as .1-age fish.

The earlier timing of the maturing group of .2-age fish indicates that they segregate from those not maturing, apparently by accelerating their speed or by taking a shorter route. As .1-age fish the previous summer they had been thoroughly mixed with the immature group, as verified by the fact that .1-age immature fish tagged in the same purse seine set frequently yield Bristol Bay returns both 1 year and 2 years later (Hartt, 1966).

The summer migrations of the .2-age immature sockeye salmon can be illustrated more completely by tag returns from U.S. tagging in 1964 (fig. 16).

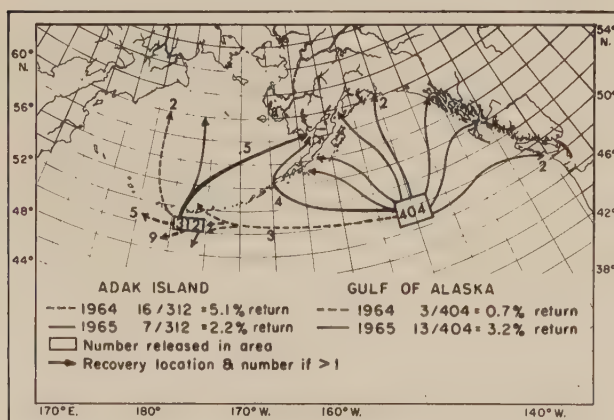


FIGURE 16.—Recovery distribution of sockeye salmon tagged as .2-age immature fish in 1964 (the arrows depicting returns in 1965 are merely drawn for convenience and are not intended to show migrations during the full year at liberty).

In 1964, substantial numbers of .2-age immature fish were tagged in the central Aleutian area and in the central Gulf of Alaska, so that together the tag returns bring out the salient features of migration. The 312 fish tagged south of Adak Island were released between late June and mid-August and were part of the characteristic summer migration that passes westward south of the Aleutian Islands. The 16 high-seas recoveries in 1964 (late July and early August) illustrate the westward and northwestward summer migration of immature fish into the western North Pacific and Bering Sea. The high-seas returns of mature fish in 1965 were probably en route to Bristol Bay, and the five Bristol Bay coastal returns together with a lack of coastal returns from areas other than Bristol Bay illustrate that fish migrating south of the Aleutians were primarily of Bristol Bay origin. The 404 fish tagged in the central Gulf (fig. 16) were released during May 1964, at which time the enclosed area was the apparent center of abundance of .2-age immature sockeye salmon as judged by longline sampling throughout the Gulf. The four coastal returns from Bristol Bay in 1965 demonstrate the presence of this stock and the nine Gulf coastal returns indicate a mixture of all major Gulf of Alaska stocks as well. The three high-seas returns in 1964 near the central Aleutians, all in late July and early August, show that part of the group from the central Gulf entered the mass westward migration south of the Aleutians. In all probability these fish were the Bristol Bay components of the Gulf mixture, and, thus, illustrate the summer return migration from the Gulf of at least some of the Bristol Bay immature fish. The route followed by the Gulf of Alaska stocks is not known, but they apparently did not enter the migration south of the central Aleutians, since tagging in that area yielded no Gulf coastal returns. Thus, the data in figure 16 illustrate that the migratory course of different salmon stocks can be discrete even though they overlap at certain times and places, which in turn suggests inherently different responses to whatever cues may be guiding them even at the immature stage.

The migrations of the .2-age immature sockeye salmon during the remainder of their third year at sea are apparently a repetition of those in their second year, i.e., westward or northwestward into

the western North Pacific and Bering Sea during summer and fall, and then southward and eastward in the Subarctic Current in winter and spring (fig. 11E). During summer and fall they are mixed with the .1-age group of the next younger generation, and in winter they are joined by the newest generation of juveniles coming from Bristol Bay as discussed earlier. Finally, at the end of their third year and the beginning of their fourth summer, they again migrate westward in the Alaska Stream, northward through the Aleutian passes and northeastward to Bristol Bay. As .3-age mature fish they average 57 to 59 cm. in fork length and are accompanied by that part of the new .2-age group that is maturing in the same year. Their final migration is shown diagrammatically in figure 11F.

SUMMARY

A review of the entire ocean migration of Bristol Bay sockeye salmon as summarized in figure 17 indicates that they make two or three circuits of an elongated east-west course extending from about long. 165° E. to 140° W. The diagram is simplified and idealized, but it takes into account the major seasonal migrations and shifts in abundance shown by available catch and tagging data. The change in age is shown for convenience as occurring only at the western extremity of the migration, but undoubtedly each age group is distributed over a considerable part of the migratory path at the time the winter annuli are formed.

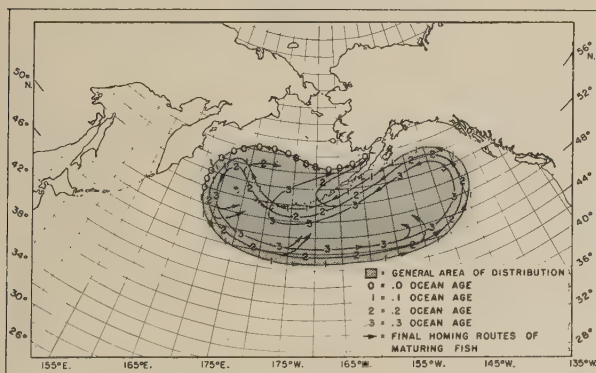


FIGURE 17.—Diagram of ocean migrations of Bristol Bay sockeye salmon based on U.S. seine catch data, and on Canadian, Japanese, and U.S. tagging data through 1966.

COMMON CHARACTERISTICS OF SALMON MIGRATIONS

We have described the principal features of the migration of three of the major stocks of salmon in the North Pacific. We have postulated migrations and behavior that seem to us to be necessary if the salmon are to migrate to where they have been found, even though our information has some significant gaps. Many of the features of the migrations and behavior of these stocks are characteristic of most salmon stocks; we will summarize them in this section before we turn to a discussion of possible direction-finding or position-finding mechanisms.

The first outstanding feature is that each individual performs the migration once with no possibility of learning from a parent and with a poor chance of spawning successfully to perpetuate the race if it becomes lost or departs from the required time schedule. Clearly the navigational system is an entirely inherited series of responses to stimuli.

Second, the salmon migrate near the surface of the ocean, mostly in the upper 10 m. The success of the Japanese high-seas fishery, which uses surface gill nets (about 5 m. deep), and the research fishing experience with gill nets and longlines indicate that the salmon are typically caught near the surface. A few salmon (mostly chum salmon) have been taken by gill nets set at depths of 30 to 70 m. (International North Pacific Fisheries Commission, Annual Report, 1960: 26), but the latter depth seems to be near the depth limit. In coastal waters, coho salmon are often taken by trollers at a depth of 10 to 20 m. and chinook salmon between 20 and 30 m. (Milne, 1955).

The third outstanding feature is the long distance traveled. The pink salmon from southeastern Alaska or British Columbia and from the Karaginski district cover 3,000 miles (5,556 km.) or more in 12 to 15 months. Some of the pink salmon from the Karaginski district travel more than 4,000 miles (7,408 km.). Even greater distances are traveled by chum salmon which return to Hokkaido from south of Kodiak and chinook salmon which return to the Columbia River from south of the central Aleutian Islands. Further, the salmon that spend more than 1 year at sea, such as the chum and sockeye salmon, may well undertake an annual feeding migration in excess of 2,000 miles (3,704 km.). Our information about such migra-

tions for immature fish is scanty, but the circumstantial evidence certainly indicates that the Bristol Bay sockeye salmon undertake substantial feeding migrations during their second and third summers at sea before they return to the home stream.

Fourth, much of the migration is not to and fro, but circular. The circuit which is closed only upon return home appears to consist of a single loop in the pink salmon from southeastern Alaska-British Columbia and Kamchatka and multiple loops in the Bristol Bay sockeye salmon. In none of these cases does it appear to be possible for the salmon to use memorized stimuli that could be followed back in reverse order.

During these long migrations the races that have been studied extensively occupy a distinctive but very large part of the ocean. Thus, the ranges of the various stocks of the several species overlap to an enormous extent. For example, tagged salmon have returned to Bristol Bay and also to the Fraser River from a group caught in a single set of the net in the northwestern part of the Gulf of Alaska. The salmon of the several species tagged near Adak Island, Alaska, have been recovered from nearly the western, northern, and eastern extremities of the range of Pacific salmon.

We believe that particular stocks of salmon have no tendency to school as a group in the ocean. We reinforce this assertion by the observation that usually we capture salmon of different species, age groups, and sizes on single sets of gear except when close to a destination of maturing salmon where a single stock may predominate. Even in such areas with a dominating single stock, the numbers caught per seine set are much more uniform over considerable areas and on successive days than would be true if the salmon were in separate, compact schools as are herring, for example.

Perhaps the most startling evidence of the individual behavior of salmon is indicated by the distribution of the mature Bristol Bay sockeye salmon in May and early June, 4 to 10 weeks before they arrive in Bristol Bay (fig. 15). At this time they are spread over some 2,000 miles (3,704 km.) of ocean in an east-west direction and some must migrate to Bristol Bay from as far as 1,200 miles (2,222 km.) away, either directly or in a dogleg to circumnavigate the Alaskan Peninsula. Within

this range no evidence has appeared of segregation of the runs to the individual Bristol Bay rivers.

The salmon appear to be nearly continuous travelers. Many of them average about 10 miles (18.5 km.) per day while immature. When maturing, they commonly travel an average of 25 to 30 miles (46.3-55.6 km.) a day and occasionally may average more than 45 miles (83.3 km.) daily over long distances.

These speeds are clearly faster than most ocean currents that may carry the fish. The directional catches of the purse seine in many parts of the ocean for both mature and immature fish indicate clearly that the salmon exceed the speed of the current. The migration is positive, not a passive drifting.

These long migrations terminate on a remarkably consistent schedule. The migration of the Bristol Bay sockeye salmon past Adak Island (about 900 miles [1,667 km.] from home) is completed in about the same length of time and in about the same sequence of individuals as the migration through the fishing areas in Bristol Bay (Hartt, 1966). The runs in Bristol Bay in 1956-65 peaked on the average date of July 5, and the earliest and latest peaks were July 2 and July 9 (Royce, 1965). Eighty percent of the run in the same years arrived in 9 to 22 days. Other runs of salmon in more southerly latitudes commonly occur over greater periods of time, but we believe this spread is usually due to different schedules of the several populations that make up these runs. It appears to be common for a single interbreeding population to keep a schedule that varies from the average by only a few days.

The arrival of the salmon is less variable than the seasonal change in the weather. For example, average water temperatures at Weather Station P, located at lat. 50° N., long. 145° W. in the central Gulf of Alaska, show an average monthly increase of 2.2° C. from May to July (Bureau of Commercial Fisheries, 1957-65), but the range of attained mean monthly temperatures for 1957-65 shows that the May mean varied from 6.1° to 7.8° C., the June mean from 7.8° to 10.6° C., and the July mean from 10.6° to 13.3° C. If the timing of salmon migrations were governed by certain critical temperatures in the waters through which they are distributed, then the arrival date would vary by about 2 weeks around a mean.

The routes followed during the migrations seem unrelated to land or continental shelves. Sometimes a considerable concentration of salmon appears in passes and near points, but the normal migratory routes seem to be across open water, even where, as in the approaches to inner Bristol Bay, it would be convenient to follow close to the shore.

The remarkable directness of the final migration in the open sea is illustrated by the Karaginski district pink salmon that migrate through the area of the Japanese high-seas fishery. When the fish have been tagged and released from different points along a north-south line, the recaptures show the tendency to proceed rather directly toward their destination (fig. 8). Obviously, their migration is not random as suggested by Saila and Shappy (1963).

Many of the migration routes traverse different ocean domains. The Karaginski pink salmon, for example, within 2 months apparently travel from the eastwardly flowing central Subarctic Current across the Alaskan Gyre, across the westerly flowing Alaskan Stream, and through the Bering Sea Gyre in the western Subarctic Domain (see Dodi-meade et al., 1963:167). Bristol Bay sockeye salmon regularly occupy the Alaskan Gyre and the western Subarctic Gyre in late spring and migrate through the Bering Sea Gyre on the homeward migration. Such routes clearly take the salmon through parts of the ocean far removed from any recent mixing with home-stream waters, and we conclude, as does Neave (1964), that the olfactory sense cannot provide a significant source of guidance information except at the end of the route.

Much of this migration takes place through and during some of the most prolonged and violent ocean storms in the world. The weather of the Aleutians area (U.S. Department of Commerce, 1955: 343) is characterized by persistently overcast skies, high winds, and violent storms. No other oceanic area in the world is recognized as having worse weather in general than that of the Aleutian Islands—clear weather over large areas is rare. Even in the milder summer periods, the sky is obscured by fog, mist, haze, or clouds most of the time. In the outer parts of Bristol Bay (U.S. Department of Commerce, 1955:631) the average weather in June (the month when most salmon are homeward bound) is 44 percent fog, mist, or haze,

and mean cloud cover is 8/10. In the central Gulf of Alaska (U.S. Department of Commerce, 1955: 619) the average June weather is 25 percent fog, mist, or haze; the mean cloud cover is 9/10. Our own experience with several years of vessel operation in this area indicates that it is impossible to navigate by celestial observations alone, and we suggest that salmon have far too little opportunity to observe the direction of either the sun or the polarization of light to keep the kind of schedule that they manage.

POSSIBLE GUIDANCE MECHANISMS

Little can be said about the physiology of salmon on which specifically explains how they navigate during transoceanic migrations, because the necessary experiments have not been performed. If certain generalizations are made, however, some interesting possibilities emerge from the migration data just presented and from the literature of fish physiology as a whole.

Two of the preceding generalizations from the tagging and seining data seem particularly significant. First, the most common direction of travel follows the various North Pacific currents. Second, salmon in the open sea do not drift with the current, but actively swim with it. We, therefore, conclude that the migrations of salmon on the high seas are actively directional in a way which somehow relates to the ocean currents. Directional cues for animal orientation have included celestial bodies, water movement, olfactory stimuli, and electrical or magnetic fields. Let us examine whether any of these are compatible with our data on salmon migrations.

SUN ORIENTATION

The sun, a prominent object by which some terrestrial animals navigate, could similarly serve salmon on the high seas. Indeed, certain lake fish have such an orienting mechanism (Hasler and Schwassmann, 1960). Also, some arthropods orient to the plane of polarization of sunlight (Ivanoff and Waterman, 1958). Arthropods and fish both require good visibility of the sun, however, because both become disoriented when clouds obscure the sun (Waterman, 1959; Hasler et al., 1958). Salmon, on the other hand, migrate at night as well as during the day and through regions where clouds obscure the sun almost continuously.

Furthermore, small lakes have only minimal amounts of wave action to complicate a fish's view of the sun, but marine fish must view the sun through a water surface which is never completely calm. Also, lake fish can migrate in straight lines; salmon migrate along circular as well as straight routes. This circumstantial evidence casts doubt on sun orientation as a primary navigational mechanism for Pacific salmon.

Although the cloudy weather of the North Pacific severely limits the possible use of sun orientation by salmon, use of the sun cannot be entirely eliminated from consideration. An oceanic bird, the slenderbilled shearwater (*Puffinus tenuirostris*), which makes an annual circum-Pacific, trans-equatorial migration, travels near the Aleutian Islands at about the same time that some salmon there begin their final homeward migration. The slenderbilled shearwater appears to use sun orientation as its primary navigational cue (Serventy, 1963), even though a related shearwater becomes disoriented during overcast conditions (Matthews, 1964). Despite such evidence on possible use of the sun, a simpler hypothesis to explain navigation by salmon on the high seas seems preferable.

ORIENTATION TO WATER MOVEMENT

Fish in rivers and streams are very sensitive to current direction and usually orient upstream to maintain position. Salmon smolts often show an active downstream orientation during their seaward migration. Optical, tactile, and lateral-line senses all seem to be involved in these rheotropisms, but the need for some kind of stationary reference point, such as a shore or the stream bottom, makes this an unlikely mechanism for use on the high seas where reference points are very distant. Direct detection of water movement also seems unlikely because of the very large size of the water bodies and, therefore, the correspondingly slight velocity gradients. A gradient does exist, however, and the sensitivity of fish to velocity gradients in the absence of other cues appears untested; it cannot be entirely excluded as a possible navigational mechanism.

Salmon are perhaps capable of detecting the interfaces between moving bodies of water either through sensing of chemical differences between two bodies of water or by detecting the water tur-

bulence at the interface. This navigational cue would lead to a great deal of random swimming, however, while the fish searches for these margins and would tend to concentrate fish near the margins of ocean currents; neither behavior is characteristic of salmon migration. Salmon are relatively evenly distributed across the ocean currents and the migration routes appear well defined and "purposive," often converging on the spawning streams from several directions.

ELECTRICAL POTENTIALS AVAILABLE FOR ORIENTATION

Because sea water is an electrical conductor moving through the earth's magnetic field, the production of an electrical voltage can be expected. Oceanographers have recognized the electrical potential of sea water for some time. Stommel (1954) found potential differences of 0.2 to 2.6 v. across long distances in the Atlantic Ocean among several submarine cables. Similar voltages were observed between Florida and Cuba. Snyder (1966), in describing the underwater search for the atomic submarine *Thresher*, reported a voltage of about 140 mv. (millivolts) between towed electrodes, one on the surface and one in about 2,440 m. of water. Hughes (1962) attempted to use these voltages to measure ocean currents by towing electrodes, spaced 46 m. apart, behind a ship. He found voltages of 3 to 5 mv. when the ship crossed the current and a reversal of polarity when the ship traveled in the reverse direction. Voltage was nil when the ship moved either with or against the current. The voltages per knot of current varied considerably in shallow water but consistency was greater in deep water.

The electrical gradient that might be available for navigational use, therefore, is about 0.1 to 0.5 μ v. (microvolts)/cm. Because these voltages are directly related to the current and are polarized with respect to its direction, electrical cues seem to be a possible navigational device for salmon on the high seas. Magnetic sensitivity has been shown for several animals, but the receptor organ is unknown. Presumably, detection occurs as a result of a voltage induced within the receptor (Brown, Barnwell, and Webb, 1964). The basic question, therefore, is whether fish can detect minute voltages.

ELECTRICAL SENSITIVITY OF FISH

At present no information appears to be available on the electrical sensitivity of salmonids. Even though experiments in the electrical guidance of salmon smolts migrating downstream have been large and intensive, this work seems not to have included any examination of possible electroreceptor organs. Certain other fish, however, which have electric organs as well as electrical receptors have been investigated extensively.

One group of electric fish includes the electric eel. Hagiwara, Szabo, and Enger (1965a) described the physiological properties of electroreceptors in the electric eel, *Electrophorus*. Two types of electroreceptors reside in the lateral line. Some of them respond only to electrical stimuli, but others are mechanically and electrically sensitive. The threshold of the "pure" electroreceptors to imposed square pulses was 2 to 30 mv./cm. and the discrimination threshold was 1.5 to 5 mv./cm. Since the electric eel's low-voltage pulses that it uses for electrolocation are still relatively high voltages—20 to 50 v.—Hagiwara et al. (1965a) suggested that the response of the mechanoreceptors to these electric signals may be only incidental and not biologically significant. Because salmon hardly experience signals of this magnitude, however, more useful interpretations can be gained from information on a group of weakly electric fish.

Members of several genera of the weakly electric gymnotid eels have electric organs that produce electrical pulses of about 30 mv. at 40 to 600 per second. Lissmann (1951) recorded such signals from *Gymnarchus* and played back the fish's own signals through a pair of electrodes in the water at a distance from the fish. At a strength of about 30 μ v. the fish responded to the signals by immediately attacking the electrodes. Lissmann and Machin (1958) performed behavioral experiments with *Gymnarchus* which indicated that the fish discriminated changes in the electrical field of 0.02 μ v./cm.

In contrast, the sensitivity of individual receptors is much less than that indicated by behavioral experiments. Hagiwara and Morita (1963), who recorded electrical activity from individual neurons of the lateral-line nerve in two other gymnotids, *Staetogenes* and *Gymnotus*, found a threshold for an imposed electrical field of about

10 mv./cm. along the long axis and a discrimination threshold of 0.1 to 1 mv./cm. Hagiwara et al. (1965b) found that the electroreceptors of *Sternarchus* responded phasically and tonically to stimuli. The rate of response was highest in the presence of a metal conductor and lowest in the presence of a plastic plate over the receptor. When an electrical field was applied between head and tail, response rate changed for different polarities. At the site of greatest electrical sensitivity they found only one kind of sensory organ. The organ included several cells grouped around a single opening on the lateral line and innervated by a single sensory nerve fiber.

Enger and Szabo (1965), who recorded electrical activity in the medulla of several gymnotids, concluded that tonic responses can yield information to the fish about the presence and position of objects within the electric field and that phasic responses give information on movement, direction of movement, the size of an object, and the position of the front edge of that object. Dijkgraaf (1963) described the electrical sensitivity of the gymnotid group as about 0.05 μ v./cm. or 0.05 μ amps. (microamperes). Machin (1962) concluded that such small signals could be distinguished from background "noise" if about 40,000 receptors were involved and that this was a reasonable number of electroreceptors which might occur in the lateral-line system. Thus, it appears reasonable to conclude that at least some fish possess electroreceptors of adequate sensitivity to detect and determine the polarity of electrical voltages of the magnitude produced by ocean currents.

PREDICTION OF ELECTRICAL SENSITIVITY FOR SALMON

As indicated above, no investigations are known concerning the electrical sensitivity of adult salmon or of the presence of receptor organs in the lateral line of salmon which might be electrically sensitive. In his recent review of lateral-line function, however, Dijkgraaf (1963) came to several conclusions that might apply to salmon. His first suggestion was that the basic electroreceptor organ is a modified mechanoreceptor which has achieved maximal response to electrical stimuli. Secondly, because electrical receptors occur in the lateral line of several widely separated groups of fish, he suggested that they may have evolved

independently several times. It would appear that any fish that has lateral-line organs possessing even secondary electrical sensitivity could develop an electronavigation system relatively easily and quickly. For example, the galvanotropism of the catfish *Parasilurus* (Abe, 1935) seems to be such a development. Although we have no physiological information to confirm electronavigation on the high seas for salmon, the circumstantial evidence described above indicates that it should be included among the more likely sensory mechanisms that salmon may use during their travels.

CONCLUSIONS ON GUIDANCE MECHANISMS

We believe that the salmon's migration cannot be performed if they migrate or drift at random, or if they depend on any memorized visual or olfactory cues at any time except during the final location of the home estuary and stream. We note that the salmon predominantly travel actively with the ocean currents in circular migration routes. Many races could accomplish their migrations by moving down or across currents until close to the mouths of their home streams, where they might recall memorized olfactory cues. We note also that ocean currents produce electric potentials in a range which some fish can detect. We suggest, therefore, that salmon may depend on electromagnetic cues from ocean currents. We suggest further that their response to all migratory cues is inherited, not, memorized.

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HYDROLOGICAL AND BIOLOGICAL CHARACTERISTICS OF FLORIDA'S WEST COAST TRIBUTARIES¹

BY ALEXANDER DRAGOVICH,² JOHN A. KELLY, JR.,³ AND H. GRANT GOODELL⁴

ABSTRACT

Data are given for 10 stations in the Hillsborough, Alafia, Little Manatee, Manatee, Myakka, Peace, and Caloosahatchee Rivers, which flow into west Florida bays. Variations in temperature, salinity, chlorophyll "a," dissolved oxygen, total phosphorus, inorganic phosphate-phosphorus, copper, and iron were recorded over a 13-month period. The variations are discussed in terms of differences in precipitation, river discharges, and general geological properties of river basins. Certain hydrological conditions of the tributaries are compared with the conditions of the adjacent neritic waters of the Gulf of Mexico.

Thermal differences between surface and bottom were negligible. The temporal distribution of salinity was influenced by precipitation. Distribution of total phos-

phorus and inorganic phosphate-phosphorus was related to the underlying phosphatic formations of the various river basins. Maximum values of total dissolved oxygen occurred in winter and minimum in summer; no anaerobic conditions were encountered. Concentrations of chlorophyll "a," copper, and iron were higher in the rivers than in the adjacent sea.

The quantity of nutrients contributed by rivers to the sea is determined largely by the volume of river flow, not by the actual concentrations of the nutrients. The possible relation between the mean input of various materials by the tributaries, and the presence of the Florida red-tide organism, *Gymnodinium breve* Davis, was tested. A correlation between iron and *G. breve* was significant at the 80-percent level.

Ecological studies were made of the waters of Tampa Bay, Charlotte Harbor, and the adjacent Gulf of Mexico as part of an investigation of the Florida red-tide organism, *Gymnodinium breve*. Red tide in waters along the southwest Florida coast is associated with dense concentrations of *G. breve*, discolored water, and fish kills.

Red tides throughout the world occur primarily in coastal areas and usually in periods of heavy rainfall and increased river discharge. The presence and growth of phytoplankton in coastal waters depend largely on the quantity and quality of inorganic and organic nutrients, particularly trace metals and external metabolites (Provasoli, 1958).

Rivers make annual additions of nutrients to the sea. In evaluating the effects of Florida west coast tributaries on red-tide outbreaks and estuarine productivity, a thorough knowledge of the hydrology of the tributaries may be helpful. Because published information on the hydrology of these streams is limited, a survey was undertaken to assess hydrological characteristics of seven major rivers that flow into Gulf estuaries. Dragovich and May (1962) listed publications concerned with the hydrology of streams of the west coast of Florida.

We studied monthly variations in certain hydrological and biological properties of the Myakka, Peace, and Caloosahatchee Rivers which enter the Charlotte Harbor estuarine system. These streams were selected because of their importance to red-tide problems and coastal oceanography. The Hillsborough, Alafia, Little Manatee, and Manatee Rivers, which are tributaries of Tampa Bay, were included because new ecological factors were added to those measured

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in previous studies (Dragovich and May, 1962).

Temperature, salinity, chlorophyll "a," oxygen, total phosphorus, inorganic phosphate-phosphorus, copper, and iron were measured.

Copper was included in our past studies and in the present one because its high toxicity to laboratory cultures of *G. breve* suggested that it

might be a limiting factor in the physiology of this species in natural waters. It was determined only in the Myakka, Peace, and Caloosahatchee Rivers because earlier studies in Tampa Bay tributaries revealed that the concentrations there were nontoxic to *G. breve* (Dragovich and May, 1962).

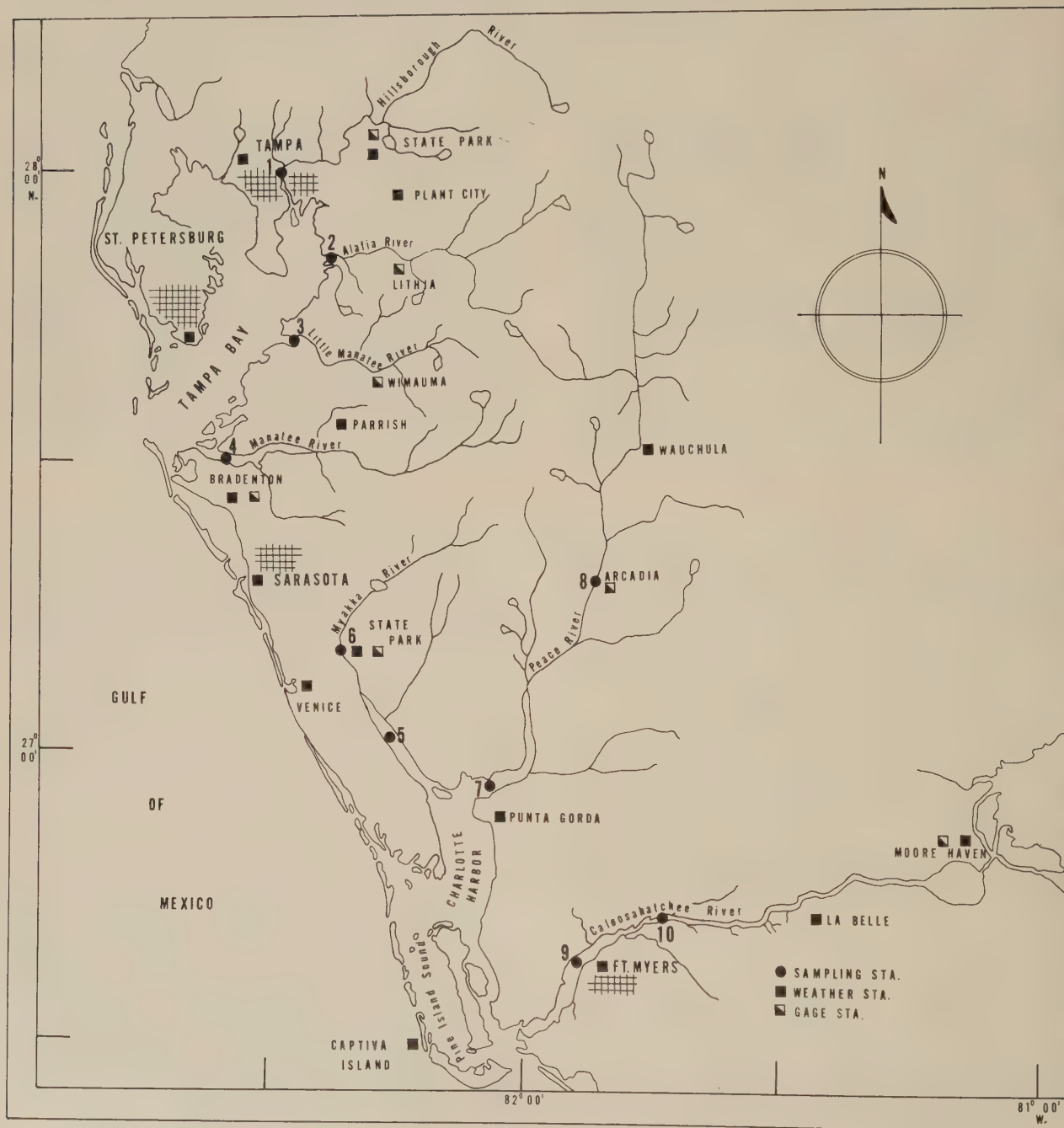


FIGURE 1.—West coast of Florida showing rivers, sampling locations, and weather and gage stations.

SAMPLING PROCEDURES AND LABORATORY TECHNIQUES

The study began in January 1964 and continued through January 1965. The sampling consisted of monthly collections of water samples near the surface and bottom at 10 stations (fig. 1). Station depths ranged from 1.8 to 4.6 m. Water samples at all stations were collected with a modified Van Dorn sampler (Van Dorn, 1957). Samples for total phosphorus and inorganic phosphate-phosphorus were immediately put into 200-mm. culture vials capped with polyethylene-lined screw-caps, and quick-frozen. Samples for the determination of copper and oxygen were transferred into 250-ml. glass-stoppered bottles, and for salinity into 113-ml. prescription bottles. Water samples for the determination of iron and chlorophyll were placed in polyethylene containers and sterile 500-ml. Erlenmeyer flasks.

The following physical and chemical methods of analysis were employed:

Water temperature—mercury thermometer calibrated to the nearest 0.1° C.

Salinity—Mohr-Knudsen method (Knudsen, 1901).

Inorganic phosphate-phosphorus—Robinson and Thompson (1948) method.

Total phosphorus—Harvey (1948) method.

Total dissolved copper—Hoste, Eeckhout, and Gillis (1953) method.

Total iron—Armstrong (1957) method.

Dissolved oxygen—Winkler method (Jacobsen, Robinson, and Thompson, 1950).

Chlorophyll "a"—Richards and Thompson (1952) method.

Samples for copper analysis were filtered, but not those for total phosphorus and iron. The iron and total phosphorus values represent the respective elements in true solution and particulate form combined.

DISTRIBUTION OF METEOROLOGICAL, HYDROLOGICAL, AND BIOLOGICAL PROPERTIES

PRECIPITATION

Data on precipitation are from the Annual Summary of Climatological Data, 1964, prepared by the Environmental Science Services Administration, U.S. Department of Commerce. Stations used were: Tampa, Hillsborough River State Park, and Plant City for the Hillsborough

and Alafia Rivers; St. Petersburg, Parrish, and Bradenton for the Little Manatee and Manatee Rivers; Sarasota, Venice, and Myakka for the Myakka River; Wauchula and Punta Gorda for the Peace River; and Captiva Island, Fort Myers, La Belle, and Moore Haven for the Caloosahatchee River (fig. 1).

From January 1964 to January 1965 the mean annual precipitation was 135.1 cm. for Tampa Bay and 108.2 cm. for the Charlotte Harbor-Pine Island Sound area. The period July through September contributed 54 percent and February 10.5 percent of the total precipitation. Minimum and maximum mean monthly precipitation values were 6.6 cm. and 267.5 cm. in the area of the Hillsborough and Alafia Rivers.

RIVER DISCHARGE

The office of the U.S. Geological Survey, Branch of Surface Water, Ocala, Fla., supplied information on river discharges at seven stations (fig. 1). These stations gave a combined flow of 2,566,729,830 m.³ from all rivers from January 1964 through January 1965 (grand total discharged). Volumes of water were highest in the Hillsborough and Peace Rivers (figs. 2, 8, and 9). River flow was highest in periods of heavy rainfall (figs. 2-11).

SALINITY

Only two stations (6 and 8) possessed limnetic characteristics throughout the period of study. Salinities at the remaining stations ranged from 0.12 p.p.t. (parts per thousand) at stations 9 and 1 during the rainy season to 28.93 p.p.t. at station 4 in May just before the onset of the rainy season.

The true temporal and vertical distribution of salinity cannot be assessed from these observations because the samples were collected without regard to tidal stage. Nevertheless, the rainfall-river discharges and salinity showed a close inverse relation (figs. 2, 4, 6, and 11). At a few stations (1, 5, and 10) salinity reached 0.12 p.p.t. during, or immediately following, periods of heavy rainfall.

The difference in salinity between the surface and bottom at all stations varied from 0 to 13.11 p.p.t. Vertical mixing was relatively good at stations 4, 5, 7, 9, and 10. The most pronounced vertical differences of salinity were at stations 1, 2, and 3, near the mouths of the Hillsborough, Alafia, and Little Manatee Rivers.

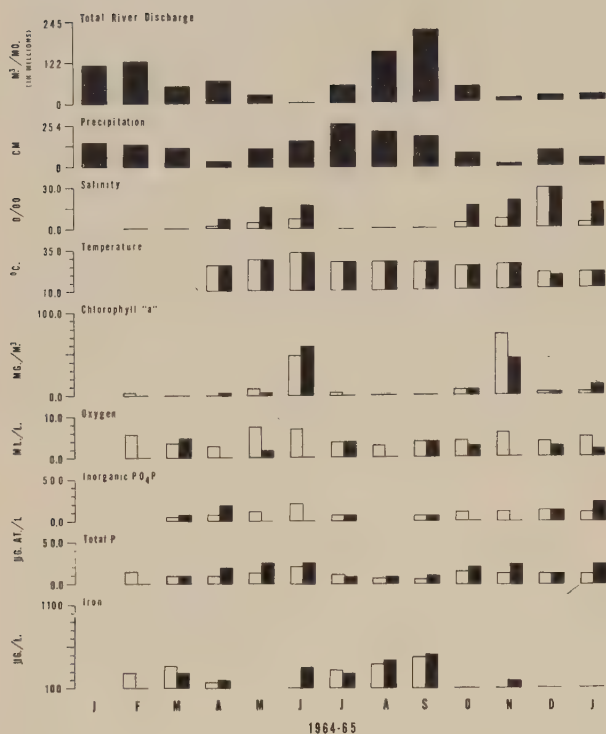


FIGURE 2.—River discharge, precipitation, and hydrological properties at station 1, Hillsborough River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

Salinity is a limiting factor in the distribution of many marine and estuarine organisms, but reliable data on the relation of estuarine organisms to salinity are scarce (Gunter, 1961). The unstable salinity at most stations was an ecological barrier to stenohaline and to some euryhaline organisms. Conditions were suitable only to forms that can exist over the entire salinity range from fresh water to sea water.

Since the favorable salinity range for the growth of *Gymnodinium breve* lies between 21 and 37 p.p.t. (Rounsefell and Dragovich, 1966), salinities at the river stations were seldom favorable for its growth.

TEMPERATURE

The annual temperature ranges during this study were the observed tolerance ranges for fishes (Springer and Woodburn, 1960) and invertebrates (Dragovich and Kelly, 1964) in Tampa Bay and for resident biota in Florida Bay (Tabb and Manning, 1961).

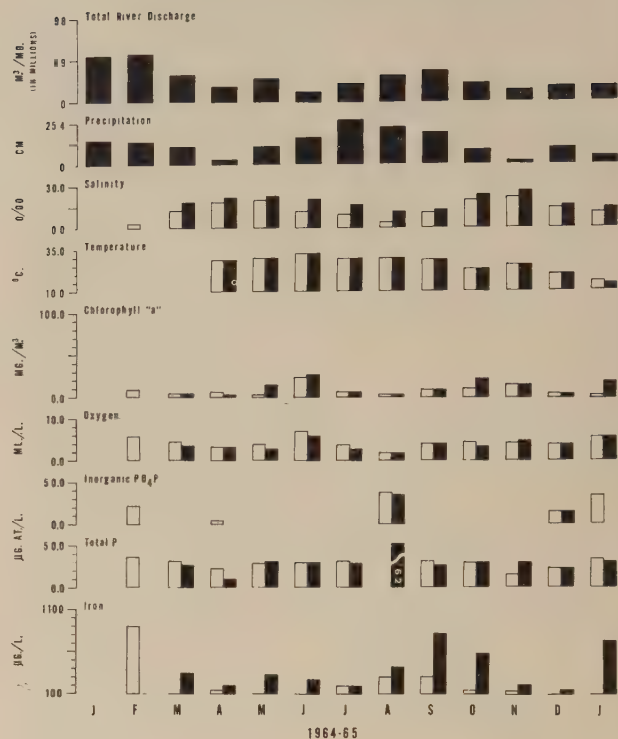


FIGURE 3.—River discharge, precipitation, and hydrological properties at station 2, Alafia River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

The water temperature varied from 12.8° to 32.4° C.; monthly changes in all rivers and stations were similar (figs. 2–11). Temperatures were high from April through September (highest in June and July 1964), and low in December, January, and February (lowest in January 1965).

Temperature differences between surface and bottom were less than 0.5° C. in about 92 percent of the observations; twice they exceeded 1° C. Temperatures at the stations with brackish water were affected by displacement of water masses during tidal oscillations.

CHLOROPHYLL "a"

Concentrations of chlorophyll "a" varied from 1.3 to 245.5 mg. per cubic meter. The highest individual and mean values for the entire period were at station 8 in the Peace River (fig. 9), where mean surface and bottom concentrations were 82.3 and 49.2 mg. per cubic meter. At other stations, corresponding values varied from 3.9 to

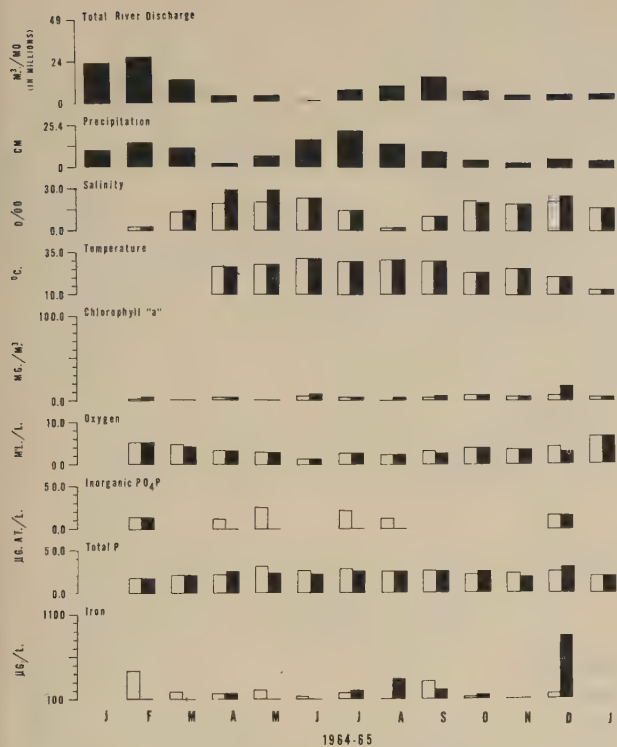


FIGURE 4.—River discharge, precipitation, and hydrological properties at station 3, Little Manatee River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

17.9 mg. per cubic meter; in 74 percent of the observations they were below 10 mg. per cubic meter.

The temporal distribution of chlorophyll "a" was dissimilar between stations (figs. 2–11). The expected peaks during phytoplankton blooms in the spring or fall did not appear at all stations. The production was lowest in February, March, May, July, and August 1964 and in January 1965.

Concentrations of chlorophyll "a" at all river stations were higher than the corresponding values in the adjacent Gulf of Mexico (table 1). The extremely high means for surface and bottom at the upstream station in the Peace River were 30.2 and 17.8 times greater than the corresponding values from the upper section of Charlotte Harbor. The mean surface concentration of chlorophyll "a" at this river station was comparable to the maximum reported from East Lagoon, Galveston, Tex., and higher than the mean values reported from Alligator Harbor and the Dry Tortugas, Fla. (table 2).

The mean values of chlorophyll "a" in Tampa Bay tributaries were highest in the Hillsborough

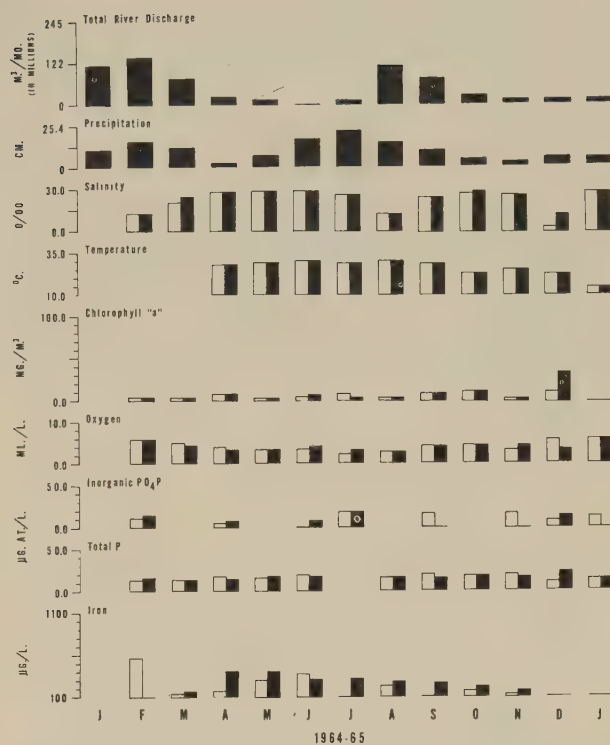


FIGURE 5.—River discharge, precipitation, and hydrological properties at station 4, Manatee River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

and Alafia Rivers (table 1). Except for the Hillsborough River, the mean chlorophyll "a" values in Tampa Bay tributaries were similar to those in upper Tampa Bay but lower than those from East Lagoon, Tex., and Alligator Harbor, Fla. (table 2).

The dissimilarity among stations in production of chlorophyll "a" may have been caused by a combination of factors. Zein-Eldin (1961) attributed the vertical gradient of chlorophyll "a" in East Lagoon to tidal oscillations and turbulence. The fact that mean concentrations were lower at the river mouths of the Hillsborough, Alafia, and Little Manatee Rivers than in Hillsborough Bay favors this view.

PRODUCTION OF ORGANIC MATTER

The rate of organic production in tributaries was estimated from the following equation (Ryther and Yentsch, 1957):

$$P = \frac{R}{K} \times C \times 3.7$$

TABLE 1.—Mean concentrations of chlorophyll "a," iron, and inorganic phosphate-phosphorus in Florida west coast tributaries and adjacent bays and neritic waters of the Gulf of Mexico, January 1964 to January 1965

[S=surface; B=bottom]

Location	Chlorophyll "a"		Iron		PO ₄ -P	
	S	B	S	B	S	B
<i>Tampa Bay area</i>						
Rivers:	mg./m. ³	mg./m. ³	μg./l.	μg./l.	μg. at./l.	μg. at./l.
Hillsborough	12.41	12.03	202.4	235.0	9.6	19.1
Alafia	8.13	12.04	216.6	381.0	33.6	29.1
Little Manatee	3.92	5.05	187.5	219.0	22.2	24.8
Manatee	5.44	7.68	217.0	251.6	15.1	16.6
Bays:						
Old Tampa Bay	5.56	9.40	115.0	-----	23.2	25.8
Hillsborough Bay	30.22	19.47	147.8	-----	24.4	24.0
Upper Tampa Bay	6.78	7.37	74.1	-----	22.2	24.0
Lower Tampa Bay	3.14	3.37	40.6	-----	14.5	16.4
Gulf:						
9.3 km. off Tampa Bay	1.17	1.03	16.3	19.4	2.6	3.2
18.5 km. off Tampa Bay	3.78	0.95	-----	-----	1.4	0.9
27.8 km. off Tampa Bay	0.50	.54	-----	-----	0.6	1.8
37.1 km. off Tampa Bay	.36	.58	6.0	5.3	.4	.6
<i>Charlotte Harbor area</i>						
Rivers:						
Myakka:						
Station 6	7.18	6.76	622.9	683.0	9.6	7.1
Station 5	5.25	5.79	299.2	434.3	6.3	7.2
Peace:						
Station 8	82.28	49.93	460.6	490.4	32.6	30.7
Station 7	8.74	9.89	329.7	305.9	18.6	18.4
Caloosahatchee:						
Station 10	10.65	13.53	265.8	535.5	2.4	4.4
Station 9	12.13	17.94	320.9	414.3	6.2	6.4
Bays:						
Upper Charlotte Harbor	2.73	2.80	111.9	111.6	11.5	9.3
Lower Charlotte Harbor	2.37	2.28	93.3	76.4	10.4	5.8
Gulf:						
9.3 km. off Boca Grande	1.86	1.28	26.0	20.3	1.6	1.1
18.5 km. off Boca Grande	.95	.53	-----	-----	.7	1.0
27.8 km. off Boca Grande	.54	.42	-----	-----	1.0	.7
37.1 km. off Boca Grande	.28	.29	16.5	4.6	.7	.6

TABLE 2.—Reported concentrations of chlorophyll "a" in coastal and marine areas of the Atlantic Ocean and the Gulf of Mexico

Location	Concentration		Reference
	Mean	Maximum	
East Lagoon, Galveston, Tex.	mg./m. ³ 17.6	mg./m. ³ 84.6	Zein-Eldin (1961).
Alligator Harbor, Fla.	4.3	14.0	Marshall (1956).
Florida coastal waters	-----	30.7	Marshall (1956).
Dry Tortugas, Fla.	0.3	-----	Riley (1938).
North Atlantic	-----	2.5-3.6	Riley (1939).

¹ This value was observed in the midst of bloom of *Gymnodinium breve*.

where P is the productivity rate in grams of carbon per square meter per day, R is the radiation factor found from the graphs of Ryther and Yentsch (1957), K is the extinction coefficient of the water, and C is grams of chlorophyll "a" per cubic meter. Because the derived carbon

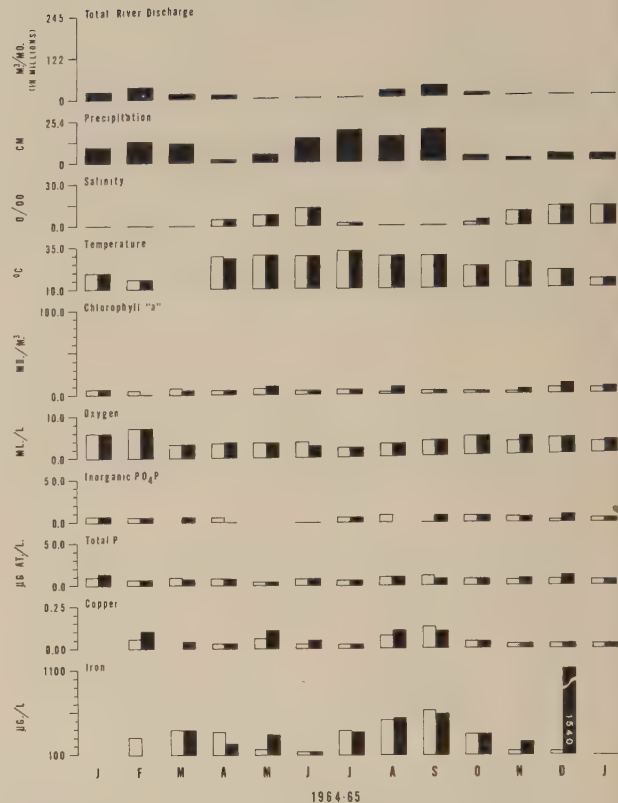


FIGURE 6.—River discharge, precipitation, and hydrological properties at station 5, Myakka River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

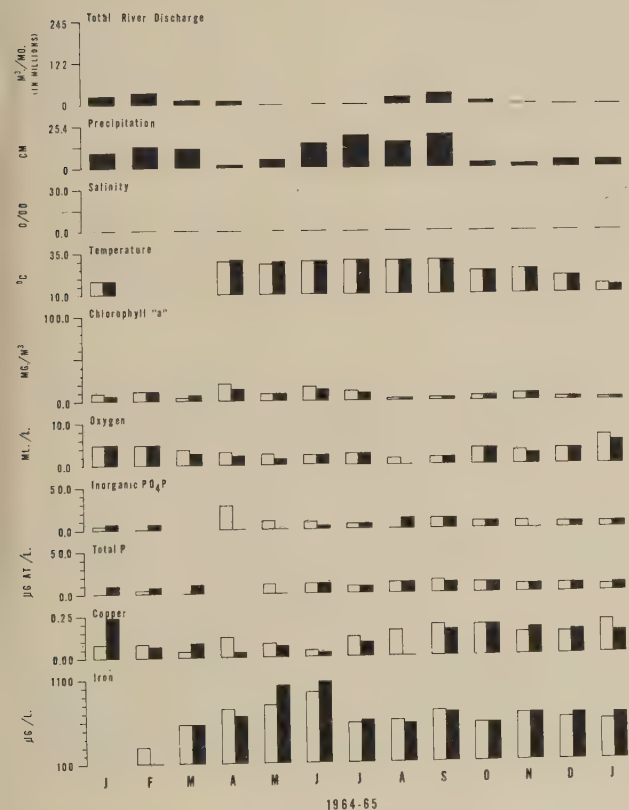
quantities are based primarily on chlorophyll values, their relative values and temporal and areal distribution resemble those of chlorophyll "a." The mean approximations of organic production exceed the analogous values (0.27 g. per square meter per day) from East Lagoon, Tex. (table 2).

The rivers contributed a substantial quantity of organic matter to the adjacent sea (table 3). Included are endocrine products liberated in the process of chlorophyll synthesis (Provasoli, 1958). The fate of these metabolites is not known, but they may have a bearing on the genesis of phytoplankton blooms and particularly of Florida red tide, if only a fraction reaches the bays and the adjacent sea. From the chlorophyll data and the river discharges, it may be deduced that quantitatively more metabolites reach the bays and adjacent sea during heavy rainfall than in periods of light rainfall.

TABLE 3.—Mean estimates of primary productivity (g. C/m.²/day) in west Florida rivers

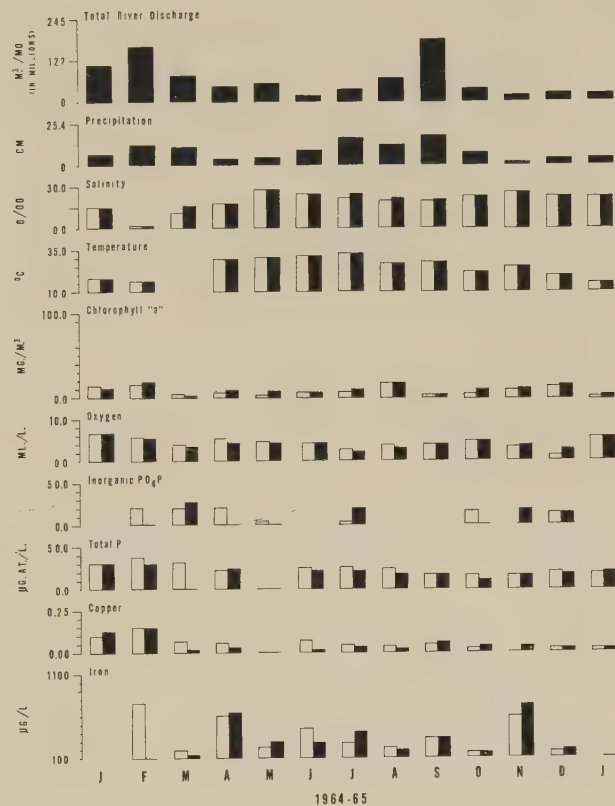
River	1964												1965	Average
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	
Hillsborough:														
Station 1		0.23	0.38	0.42	1.25	9.70	0.32	0.19	0.29	0.87	7.97	0.39	1.05	1.92
Alafia:														
Station 2		.16	1.45	1.44	2.95	9.53	1.63	1.15	2.69	4.13	3.24	.67	2.61	2.63
Little Manatee:														
Station 3		.49	.59	.83	0.44	1.10	.68	.38	.69	.91	0.67	1.40	0.39	0.71
Manatee:														
Station 4		.22	.45	.95	.38	0.69	.62	.48	.97	1.10	.39	1.92	.12	.69
Myakka:														
Station 5	0.90	.57	1.19	1.05	1.58	.64	.74	.93	.46	.46	.55	1.18	1.18	.87
Station 6	.39	.84	.51	2.00	1.03	1.81	1.10	1.41	.33	.59	.66	.37	.27	.87
Peace:														
Station 7	1.49	2.33	.79	1.54	1.21	1.34	1.54	2.91	.56	1.12	1.42	1.89	.64	1.44
Station 8	8.36	4.29	3.25	2.84	3.26	3.57	2.42	4.13	1.30	25.14	24.58	8.26	4.77	7.39
Caloosahatchee:														
Station 9	2.42	8.40	3.40	1.02	1.27	1.04	1.26	1.95	1.08	4.67	.97	1.55	.98	2.28
Station 10	1.95	1.32	2.74	2.37	.68	1.22	1.67	1.49	.71	4.79	1.29	3.06	1.31	1.89

STATION 6



1964-65

STATION 7



1964-65

FIGURE 7.—River discharge, precipitation, and hydrological properties at station 6, Myakka River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

FIGURE 8.—River discharge, precipitation, and hydrological properties at station 7, Peace River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

DISSOLVED OXYGEN

Concentrations of dissolved oxygen at the river stations varied from 0.44 to 7.56 ml. per liter. Values were highest at most stations in

winter and lowest in June and July (figs. 4–8). Oxygen values occasionally reached 100 to 142 percent saturation during every season. Most of the high values (stations 1, 2, 7, and 8) coincided with high concentrations of chlorophyll "a."

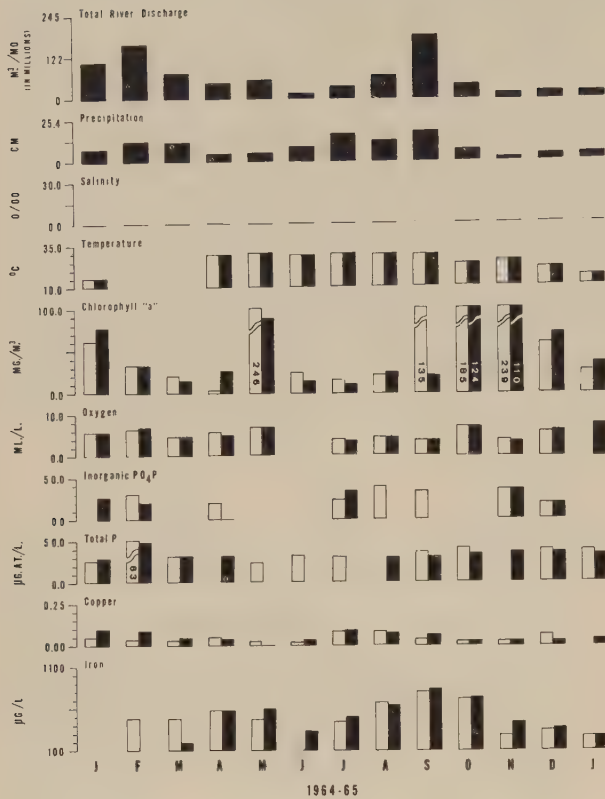


FIGURE 9.—River discharge, precipitation, and hydrological properties at station 8, Peace River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

Even though anaerobic conditions were approached several times, no complete deoxygenation was detected. In 80 percent of the observations, oxygen saturation exceeded 50 percent. Values below 50 percent in one-fifth of the observations indicated that oxygen depletion occurred in the rivers. The occurrence of 75 percent of these values from April through September suggests that the depletion was seasonal.

Differences between surface and bottom values of oxygen were less than 1 ml. per liter in 84 percent of the observations. The similarity for most of the sets of observations reflects the capacity of the river system to maintain relatively high subsurface oxygen concentrations.

Irregularities in the vertical distribution of oxygen in periods of water stratification were associated with the presence of hydrogen sulfide near the bottom. Oxygen was almost exhausted

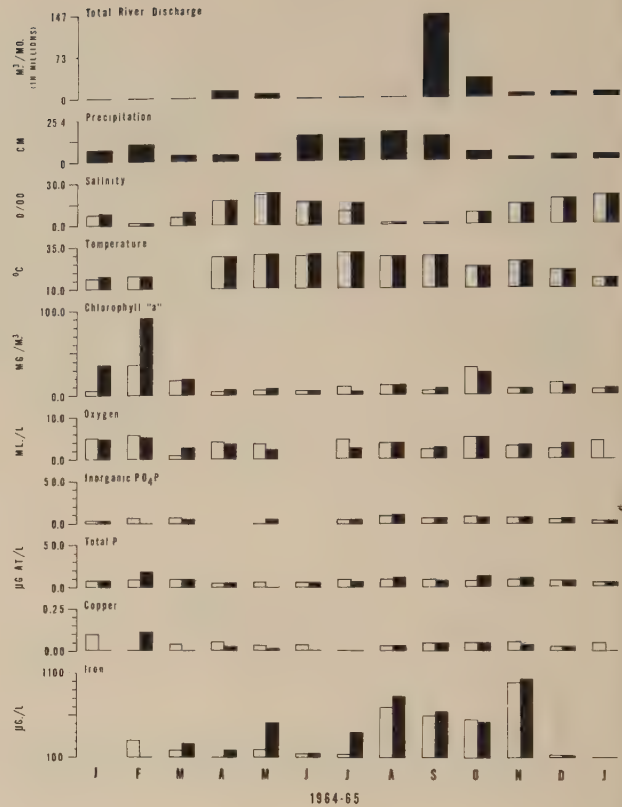


FIGURE 10.—River discharge, precipitation, and hydrological properties at station 9, Caloosahatchee River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

near the bottom in the Hillsborough River (station 1) in April, June, August, and November (fig. 2).

TOTAL PHOSPHORUS

Concentrations of total phosphorus increased from downstream to upstream stations in the tributaries of Charlotte Harbor; Tampa Bay tributaries were sampled only at the mouths of rivers.

Quantities of total phosphorus were highest in the Peace River (station 8) and second highest in the Alafia River. Mean values at the surface and bottom in the Peace River (station 8) were 35.1 and 33.3 $\mu\text{g.at.}$ per liter, and in the Alafia River (station 2) 27.5 $\mu\text{g.at.}$ per liter, and 28.7 $\mu\text{g.at.}$ per liter. At the remaining stations, the values for surface and bottom ranged from 4.2 to 23.5 $\mu\text{g.at.}$ per liter. Values were lowest at the upstream station (10) in the Caloosahatchee River.

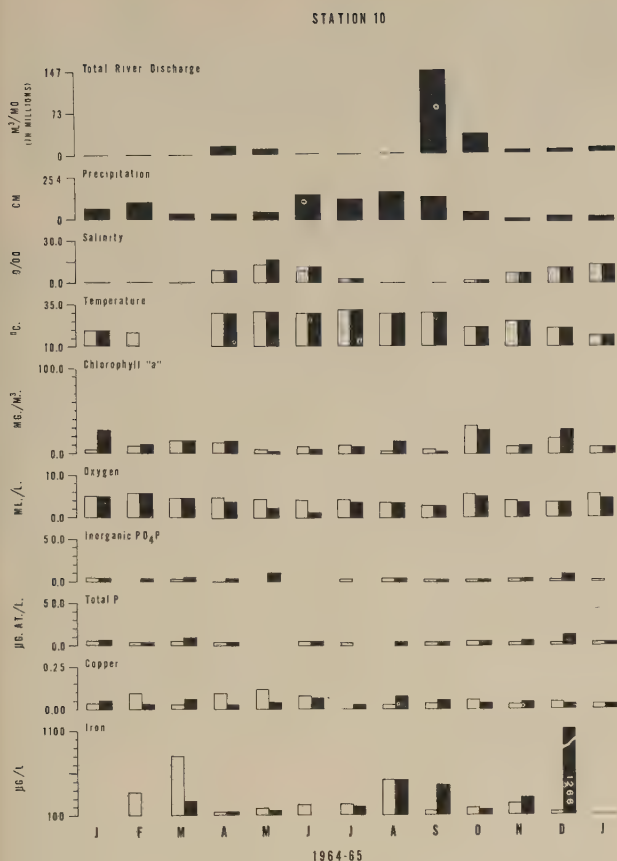


FIGURE 11.—River discharge, precipitation, and hydrological properties at station 10, Caloosahatchee River, Fla., January 1964 to January 1965. (Open bars=surface; solid bars=bottom.)

Concentrations of total phosphorus in individual samples for all stations ranged from 3.1 $\mu\text{g.at.}$ per liter in the Caloosahatchee River (station 10) to 62.9 $\mu\text{g.at.}$ per liter in the Peace River (station 8).

The differences between surface and bottom values of total phosphorus varied from 0.0 to 15.4 $\mu\text{g.at.}$ per liter. In the Hillsborough River (station 1) values were higher near the bottom than at the surface due to upstream intrusion of Hillsborough Bay water, in which phosphorus concentrations exceeded those in Hillsborough Bay (fig. 2, table 2). Salinity differences at surface and bottom substantiate the conclusion. This observation agrees with previous studies (Dragovich and May, 1962; Odum, 1953).

Vertical differences in salinity in the Alafia River (station 2) were not reflected in a pronounced vertical stratification of phosphorus (fig. 3). Concentrations of phosphorus in the river

markedly exceed those in Hillsborough Bay (table 1). The discharge waters of the Alafia River are the chief source of phosphorus for Hillsborough Bay (Dragovich and May, 1962).

The Little Manatee River empties into the upper portion of Tampa Bay, and the Manatee River into the lower portion. Phosphorus concentrations in the upper and lower bays were similar to those in the Little Manatee and Manatee Rivers (table 1). Thus, the vertical stratification of phosphorus in these two rivers was usually moderate (figs. 4 and 5).

Phosphorus values generally were higher at the surface at stations 7 and 8. Differences between surface and bottom at stations 5 and 6 were slight. Values were higher at the bottom occasionally at both stations in the Caloosahatchee River. This situation may arise from the bottom sediment which enters the lower portion of the water column during periods of turbulence.

Monthly variations in total phosphorus showed no trend. Mean concentrations of total phosphorus at each river were multiplied by flow to estimate changes in the total monthly quantity of phosphorus. Combined calculations for all rivers showed maximum quantities in February, March, August, and September—the months with maximum runoff; values were low during the minimum runoff in June and November (table 4). It appears, therefore, that the quantity of phosphorus added to the bays and the adjacent sea depends more on volume of river flow than on concentrations of phosphorus in the streams. An exception was the Alafia River—the total quantity of phosphorus was much higher than in the Hillsborough River despite greater flow rate in the latter.

Geological formations influence the phosphorus content of the river water (fig. 12). The high phosphorus values are directly attributable to drainage areas that are highest in CaPO_4 . Quantities were highest in the Peace and Alafia Rivers which flow primarily through Hawthorne phosphatic formations. Relatively high phosphorus concentrations in the Manatee, Myakka, and Peace Rivers may be explained by the fact that they flow through phosphorus-bearing formations (Bone Valley and Hawthorne). Higher values at the Hillsborough River station result from mixing of relatively phosphorus-rich bay water with river water. Concentrations were lowest in the Caloosahatchee River, only part of which drains

TABLE 4.—Quantities of iron, total phosphorus, and copper discharged by Florida west coast tributaries

[Metric tons]

River	1964												1965	Total
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	
	Iron													
Hillsborough		33.6	15.6	12.6	1.4	0.7	15.3	56.4	100.0	4.5	1.4	1.6	1.5	244.6
Alafia		49.9	6.7	3.2	6.3	1.9	4.3	10.6	19.4	7.4	2.0	2.1	6.8	120.6
Little Manatee		10.8	2.0	0.8	0.6	.1	1.3	2.6	3.6	0.6	0.2	1.6	0.2	24.4
Manatee		7.4	1.3	.7	.6	.2	0.4	2.9	1.3	.5	.2	0.1	.1	15.7
Myakka		8.9	6.6	5.6	.6	.1	1.0	10.3	18.8	1.7	.1	.2	.3	54.2
Peace		96.2	18.0	27.6	20.9	4.0	14.1	28.1	102.1	16.8	8.1	5.8	3.1	344.8
Caloosahatchee		0.2	0.6	1.6	2.3	.1	.2	0.5	64.6	11.3	2.5	3.1	.5	87.5
Total		207.0	50.8	52.1	32.7	7.1	36.6	111.4	309.8	42.8	14.5	14.5	12.5	891.8
	Total phosphorus													
Hillsborough		49.2	15.0	29.7	14.4	2.6	16.2	35.6	55.1	22.7	6.6	7.3	10.2	264.6
Alafia		61.3	26.0	9.0	26.1	9.0	18.9	56.2	30.6	18.2	8.2	12.4	16.2	292.1
Little Manatee		12.6	7.7	3.0	3.6	0.8	5.0	5.0	8.7	3.1	1.0	2.8	1.6	54.9
Manatee		6.0	3.0	1.1	0.8	.3		5.3	3.7	1.3	0.5	0.6	0.5	23.1
Myakka	6.8	6.1	3.6	2.6	.2	.1	0.5	6.8	10.9	1.1	.1	.1	.2	39.1
Peace	90.8	216.7	72.8	38.5	36.2	12.3	27.8	48.4	137.6	30.1	11.2	18.3	15.6	756.3
Caloosahatchee	0.1	0.2	0.4	1.8	1.6	.1	.1	0.2	27.9	8.2	.9	1.6	1.0	44.1
Total	97.7	352.1	128.5	85.7	82.9	25.2	68.5	157.5	274.5	84.7	28.5	43.1	45.3	1474.2
	Copper ¹													
Myakka	0.2	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.2	<0.1	<0.1	<0.1	<0.1	0.8
Peace	.6	1.0	.2	.1	<.1	<.1	.1	.2	.6	<.1	<.1	<.1	<.1	3.1
Caloosahatchee	<.1	<.1	<.1	<.1	<.1	<.1	<.1	<.1	.4	<.1	<.1	<.1	<.1	.6
Total	.8	1.2	.2	.2	.1	.03	.2	.4	1.2	.2	.02	.05	.04	4.5

¹ All values of <0.1 in computation toward the total were not used; instead, actual values were used.

TABLE 5.—Explanation of the legend for figure 12

Geological formation	Composition
Caloosahatchee marl	Predominantly sand and shell marl.
Bone Valley formation	Phosphatic, sandy clay and gravel. Composition: 55-79% bone phosphate.
Suwannee limestone	Hard and resonant. Composition: 91-98% CaCO ₃ ; chief impurity, silica.
Buckingham marl	Impermeable calcareous clay containing small grains of phosphatic material.
Lake Pleistocene deposits	Marine and estuarine deposits less than 30.5 meters above sea level.
Lake Flint marl	Calcareous fresh-water marl.
Ft. Thompson formation	Marine shell marl and fresh-water limestone.
Tampa limestone	Fairly hard and dense. Contains a large portion of very fine sand and phosphate. Composition: 74% calcium carbonate; <24% silica; trace magnesium carbonate.
Hawthorne formation	Sandy, phosphatic limestone, and green phosphatic clays.
Citronelle formation	Sand, gravel, and clay. The clay is kaolin when mixed with sand or gravel and is commonly iron stained.

through Buckingham marl formation (mainly impermeable calcareous clay containing only small grains of phosphatic material).

INORGANIC PHOSPHATE-PHOSPHORUS

The monthly changes and areal distribution of inorganic phosphate-phosphorus in all rivers were similar to those of total phosphorus (figs. 2-11). In 85 percent of the observations, inorganic phosphate-phosphorus exceeded organic and was re-

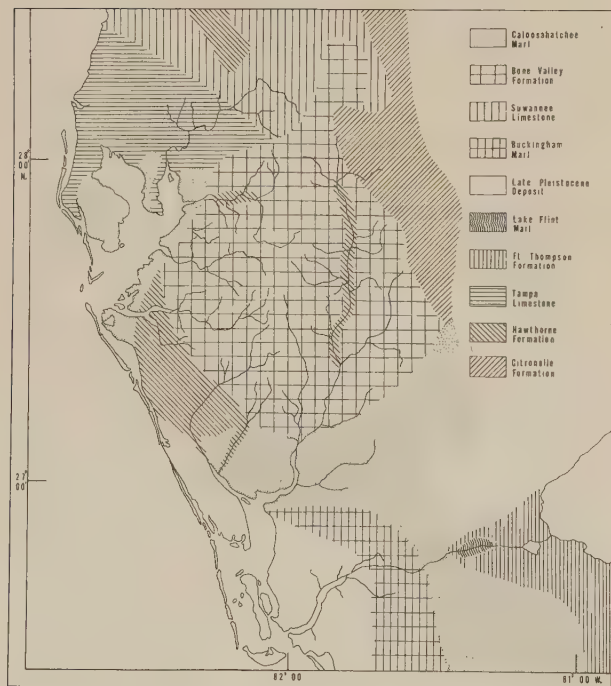


FIGURE 12.—Surface phosphate-bearing formations of the west coast of Florida (after Cooke, 1945). See table 5 for explanation of legend.

sponsible for the greater portion of total phosphorus. The quantities of phosphate-phosphorus always exceeded the minimum necessary for the growth of phytoplankters in vitro (Ketchum, 1939).

IRON

The study of the distribution of iron in Florida's west coast tributaries was undertaken for the first time in connection with the Florida red-tide studies. Thus, a few introductory remarks in regard to the importance of iron in the growth of phytoplankton seem to be appropriate. Iron occurs in many different physical and chemical forms in sea water (Ryther and Kramer, 1961). It may be present in generally unstable organic compounds that are slowly hydrolyzed in sea water (Harvey, 1937). The quantity of iron in true solution is extremely small because of the insolubility of ferric hydroxide.

The importance of iron in the physiology of phytoplankton has been stressed repeatedly (Harvey, 1957; Sverdrup, Johnson, and Fleming, 1942). Algae are able to use particulate iron as their major source of this element through ingestion by the protoplasm of particles of ferric hydroxide (Goldberg, 1952). Gran (1933) and Menzel and Ryther (1961) demonstrated the physiological dependence of phytoplankton on iron. Ryther and Kramer (1961) studied the relative iron requirements of some coastal and offshore planktonic algae. The consistency of their results demonstrates the importance of iron in determining the distribution of phytoplankton in the sea. Iron is beneficial in the culture of *Gymnodinium breve* (W. Wilson, personal communication). Even though the physiological importance of iron is known, no reliable techniques exist for determining the form in which it is available to phytoplankton (Harvey, 1937).

The concentration of iron in the sea is very small—from 0 to 10 $\mu\text{g. per liter}$ (Ryther and Kramer, 1961). Quantities of this metal are much higher in drainage waters than in adjacent seas (Harvey, 1937).

The individual concentrations of iron in our study varied from 24.2 $\mu\text{g. per liter}$ (at the surface in May at station 1, Hillsborough River) to 1540.4 $\mu\text{g. per liter}$ (at the bottom in December at station 5, Peace River). The mean values for

the entire period varied from 187.5 $\mu\text{g. per liter}$ (at the surface of Little Manatee River) to 683.0 $\mu\text{g. per liter}$ (at the bottom of Myakka River, station 6). Individual values were highest at the fresh-water stations in the Myakka and Peace Rivers and lowest in the Hillsborough River (figs. 2, 7, and 9). In 83 percent of all observations, iron values were from 50 to 599.0 $\mu\text{g. per liter}$; in 63 percent the concentrations were higher near the bottom than near the surface. The monthly changes in iron were very irregular at all stations (figs. 2–11) throughout the observation period.

Concentrations of iron in the rivers were several times higher than those in the adjacent sea and declined progressively in the seaward direction (table 1). River waters contribute iron to bay waters, but this influence is negligible offshore.

The highest concentrations of iron in the major rivers were in the area of limestone formation where the surface rock beneath the thin veneer of Pleistocene sands was either Miocene or Oligocene limestone. Iron values were intermediate in the major river (Myakka), which flows through Miocene phosphatic clays, and the difference was considerable between upriver values (station 5, fig. 6) and downriver values (station 6, fig. 7). This change can be directly attributed to the change from Pleistocene to Miocene deposits downstream. The lowest values were in the Alafia and Peace Rivers which flow through Pleistocene shelly sands of the Buckingham marl. The limestone areas are highly soluble to carbonated rain waters and carry the iron into solution with the CaCO_3 . As long as iron is in the Fe^{+2} state, it moves readily; but when it is oxidized, it is precipitated as insoluble $\text{Fe}(\text{OH})_3$. An occasional association between the increased rainfall and river discharge and higher iron concentrations was probably due to the oxidation of the iron in the limestone soils, and subsequent fixation. In times of high rainfall, iron moves into the rivers before oxidation can take place.

The total quantity of iron contributed to Gulf of Mexico waters by the rivers was estimated by multiplying average concentrations by flow. Even though monthly changes of iron concentrations at individual stations lacked a trend, combined data for all rivers showed that the contribution of iron by the rivers to the Gulf was greatest during maximum discharge (table 4).

COPPER

Concentrations of total dissolved copper at all stations varied from 0.00 to 0.23 $\mu\text{g.at.}$ per liter. The levels were highest at fresh-water station 6 (Myakka River) and lowest at station 9 (Caloosahatchee River). In 82.5 percent of the observations, copper values were below 0.09 $\mu\text{g.at.}$ per liter; 76 percent of the values that exceeded 0.09 $\mu\text{g.at.}$ per liter were in the Myakka River. Although the highest values of copper came in January (0.08 $\mu\text{g.at.}$ per liter), February (0.07 $\mu\text{g.at.}$ per liter), and September (0.08 $\mu\text{g.at.}$ per liter), at periods of high river discharge, the contribution of copper to the sea by the rivers was determined to a large extent by volume of river water, not by actual concentration. The largest total quantity of copper was contributed by the Peace River, and the lowest by the Caloosahatchee River (table 4).

Concentrations of copper were greater than those in Tampa Bay and adjacent waters of the Gulf of Mexico. The mean values for the Myakka River at station 6 exceeded those from Tampa Bay tributaries; values in the Peace and Caloosahatchee Rivers and at station 5 of the Myakka River were similar to the mean values for the Hillsborough, Alafia, and Manatee Rivers. Mean concentrations of copper were higher than those from San Juan Channel, Wash. (Chow and Thompson, 1952), but the mean concentrations at stations 5, 7, 8, and 9 are comparable with those reported by Chow and Thompson (1952) for the lower Mississippi River (table 6).

In general, changes in copper follow those of iron. This agreement results from the chemical scavenging of the colloidal $\text{Fe}(\text{OH})_3$ for copper, which is absorbed to the surface of the particles.

Copper plays an important part in biological processes of higher aquatic organisms (Vinogradov, 1953; Galtsoff, 1964; Dragovich and May, 1962); it is adsorbed by phytoplankton (Atkins, 1953) and is selectively toxic to barnacles, algae, and mollusks. The dose of copper lethal to *Gymnodinium breve* under laboratory conditions is about 0.5 $\mu\text{g.at.}$ per liter (W. Wilson, personal communication). None of the values observed in this study approached that level.

TABLE 6.—Concentrations of total dissolved copper in Florida west coast rivers, Tampa Bay, and the adjacent Gulf of Mexico waters and in the Mississippi River and the San Juan Channel, Wash.

Locality	Concentrations of copper			Reference
	Minimum	Maximum	Mean	
Hillsborough River: Station 29:	$\mu\text{g.at./l.}$	$\mu\text{g.at./l.}$	$\mu\text{g.at./l.}$	Dragovich and May, 1962.
Surface	0.02	0.07	0.04	
Bottom	.02	.09	.04	
Station 30:				
Surface	.02	.09	.05	
Bottom	.02	.08	.04	
Alafia River:				Do.
Station 31:				
Surface	.02	.16	.06	
Bottom	.03	.22	.06	
Station 32:				
Surface	.02	.08	.05	
Bottom	.01	.08	.04	
Little Manatee River:				Do.
Station 33:				
Surface	.03	.13	.07	
Bottom	.02	.12	.06	
Station 34:				
Surface	.02	.12	.08	
Bottom	.02	.13	.08	
Manatee River:				Do.
Station 35:				
Surface	.02	.11	.06	
Bottom	.02	.15	.06	
Station 36:				
Surface	.00	.16	.05	
Bottom	.01	.13	.04	
Myakka River:				Present study.
Station 5:				
Surface	.02	.12	.04	
Bottom	.02	.11	.05	
Station 6:				
Surface	.03	.17	.10	
Bottom	.02	.23	.10	
Peace River:				Do.
Station 7:				
Surface	.00	.16	.05	
Bottom	.00	.15	.04	
Station 8:				
Surface	.02	.08	.04	
Bottom	.01	.09	.04	
Caloosahatchee River:				Do.
Station 9:				
Surface	.00	.09	.03	
Bottom	.00	.11	.02	
Station 10:				
Surface	.00	.11	.04	
Bottom	.02	.11	.03	
Tampa Bay, Fla.	.00	.09	.03	Dragovich, Finucane, and May, 1961.
Gulf of Mexico adjacent to Tampa Bay.	.00	.10	.03	Do.
Mississippi River			.04	Chow and Thompson, 1952.
San Juan Channel, Wash.	.012	.06	.023	Do.

RELATION OF THE INPUT OF FLORIDA WEST COAST TRIBUTARIES TO THE ABUNDANCE OF *GYMNODINIUM BREVE*

Water samples for analysis of *G. breve* were collected each month from 22 stations in Tampa Bay, Charlotte Harbor, and the adjacent offshore waters (Dragovich and Kelly, 1966). *G. breve* was absent in samples from Tampa Bay and present

only twice in samples from Charlotte Harbor. In Gulf waters adjacent to Tampa Bay, Charlotte Harbor, and Pine Island Sound, *G. breve* was collected every month. Regression analysis was used to explore the relation between the mean monthly concentrations of *G. breve* and the weighted average input by the tributaries of Tampa Bay and Charlotte Harbor-Pine Island Sound. Weighted monthly inputs of iron, copper, phosphorus, and chlorophyll "a" for the tributaries were calculated by the formula:

$\bar{X}_{\%} = \bar{X}_I (I_{\%}) + \bar{X}_{II} (II_{\%}) + \bar{X}_{III} (III_{\%}) \dots$ etc. where $\bar{X}$ is the average value of the variable, *I*, *II*, ... at the station or river, and *I*%, *II*%, ..., the percentage of the total monthly river discharge for a particular river.

Regression analysis was chosen because its requirements are not as strict as those for correlation, in which a normally distributed population is prerequisite. Two relationships were tested—polynomial and linear multivariate regression.

In the polynomial regression, each variable (total phosphorus, copper, iron, and chlorophyll "a") was taken as the independent variable, and *G. breve* as the dependent one. The linear, quadratic, and cubic regression relationships were calculated, and each tested for significance by analysis of variance. Relationships were insignificant at the 95-percent level. At the 80-percent level, the linear regression relationship between *G. breve* and iron was significant off both Tampa Bay and Charlotte Harbor. One reason for the weakness of this relationship may be that the independent variables were not measured at the places where *G. breve* was collected.

SUMMARY

A hydrological survey of Hillsborough, Alafia, Little Manatee, Manatee, Myakka, Peace, and Caloosahatchee Rivers, west Florida, was made from January 1963 to February 1964. Monthly changes in temperature, salinity, chlorophyll "a," dissolved oxygen, inorganic phosphate-phosphorus, total phosphorus, copper, and iron were determined. Data on precipitation and river discharges and general geomorphological features of the area are also given.

The water temperature data for all rivers varied from 12.8° C. (January 1965) to 32.4° C. (June

and July 1964). Temperatures were low during December, January, and February and variably high from April through September. The vertical differences of temperature were insignificant.

Oligohaline (0.5 p.p.t. to 5 p.p.t.), mesohaline (5 p.p.t. to 18 p.p.t.), and polyhaline (18 p.p.t. to 30 p.p.t.) salinities were encountered at all but two fresh-water stations. Salinity was reduced in months of high rainfall and high river discharge.

The levels of chlorophyll "a" varied from 1.3 to 245.5 mg. per cubic meter and did not show the expected seasonal cycle of spring and autumn maximums and summer and winter minimums. The highest concentrations were in the Peace River at the fresh-water station.

No serious depletion of dissolved oxygen was indicated. In 80 percent of the observations, oxygen saturation exceeded 50 percent. Maximum values came in winter and minimums in summer. Some supersaturation was detected in every season.

Concentrations of inorganic phosphate-phosphorus and total phosphorus were high in all rivers; levels were exceptionally high in the Peace and Alafia Rivers which flow directly through an area rich in phosphatic formations. Inorganic phosphate-phosphorus was responsible for most of the phosphorus.

Copper values varied from 0.00 to 0.23 μ g.at. per liter and were higher than those in the adjacent Gulf of Mexico. They were markedly below the lethal dose for *Gymnodinium breve*.

The concentrations of iron were several times higher in the rivers than in the adjacent Gulf of Mexico waters. Values were highest at the fresh-water stations in the Myakka and Peace Rivers and lowest in the Hillsborough River. Temporal changes in iron lacked a distinct trend.

Variation in rate of flow has a marked effect on the total quantities of the materials in the rivers.

The polynomial regression between total phosphorus, copper, iron, chlorophyll "a" as the independent variable and abundance of *G. breve* as the dependent variable revealed no relationships significant at the 95-percent level; iron and *G. breve* were directly related at the 80-percent level of significance in coastal waters off Tampa Bay and Charlotte Harbor.

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INTRAGRAVEL FLOW AND INTERCHANGE OF WATER IN A STREAMBED

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ABSTRACT

The chemical quality of intragravel water in streams—the environment of salmon eggs, embryos, and alevins—is influenced by the rate of interchange of stream water and intragravel water. Factors controlling the direction and magnitude of flow or interchange of this water were identified in this study. Equations describing motion of waterflow within the streambed under specified boundary conditions are developed, and tests of the mathematical model with an electrolytic bath analog model are described.

The direction of waterflow within a streambed and the interchange of water between the bed and the stream depend primarily on the permeability, depth, and longitudinal profile of the porous streambed. Water upwells where permeability or depth of gravel decreases in the direction of streamflow and where the longitudinal bed profile is concave. Water downwells where permeability or depth of gravel increases in the direction of streamflow or where the longitudinal bed profile is convex.

Embryos and alevins of Pacific salmon (genus *Oncorhynchus*) live in gravel beds of streams for as long as 9 months before the fry emerge. The young salmon may be subjected to a poor chemical environment because of the low waterflow in the spawning bed. In laboratory experiments, oxygen privation and reduced waterflow, alone or together, impaired growth and development of salmonid embryos and caused mortality (Silver, Warren, and Doudoroff, 1963; Shumway, Warren, and Doudoroff, 1964). In natural streams, mortality of salmon spawn was high when the supply of dissolved oxygen in intragravel water (water occupying interstices within the streambed) became low (Phillips and Campbell, 1962; McNeil, 1966). Dissolved waste metabolites are known to be harmful to fishes: high levels of free carbon dioxide reduce the blood's affinity for oxygen, and un-ionized ammonium hydroxide is highly toxic to alevins (McNeil, Wells, and Brickell, 1964). The concentration of waste metabolites in the water surrounding organisms generating the wastes varies inversely with the rate of flow of intragravel water. It is, therefore, necessary that the velocity of intragravel flow be adequate to assure low concentrations of waste metabolite.

Because the primary source of oxygen and the water flowing through the gravel in many salmon spawning beds is stream water, the processes that regulate interchange between intragravel water and stream water are important in the ecology of salmon spawning beds. The purpose of my study is to identify some of the variables that control this interchange. In an earlier paper (Vaux, 1962), I related the direction of interchange to streambed shape from a mathematical model and presented field data which demonstrated that the relation was correct.

This paper treats the theory of flow of intragravel water in detail and gives the results of my laboratory experiments in which intragravel flow and interchange were simulated with an analog model. The means by which interchange can be controlled to improve water quality within salmon spawning beds are discussed.

I started my study of the movement of water within streambeds in 1958 while employed at the Fisheries Research Institute of the College of Fisheries, University of Washington. The experimental work and some of the mathematical formulation were completed in 1960–61 as part of a thesis, which was submitted to the Department

of Chemical Engineering, University of Minnesota (Vaux, 1961).

All symbols are defined the first time they appear and are listed with definitions and units in the "Notation" section near the end of this paper.

THEORY OF INTRAGRAVEL WATERFLOW

Charles Slichter (1899) first applied the mathematics of partial differential equations to the motion of groundwater (waterflow in saturated soil). His formulation of the equations describing groundwater flow provided a foundation for subsequent analyses of similar problems of intragravel waterflow.

In developing the theory of intragravel waterflow, I treat the case where the rate equation for flow in porous media is linear, i.e., conditions under which Darcy's law applies. Ergun (1952) showed that for a given particle size and bed porosity, the ratio of pressure gradient to water velocity in a porous bed is given by $(\Delta P/L)/v \propto (c_1 + c_2 N_{Re})$ where c_1 and c_2 are known constants, and N_{Re} is the Reynolds number based on particle diameter. The constants c_1 and c_2 respectively account for pressure loss from the effects of viscous and kinetic energy. The expression $(\Delta P/L)/v \propto c_1$, called Darcy's law, is considered applicable for Reynolds numbers less than unity (Rumer, 1965). Although flow may be laminar in situations where the Reynolds numbers are higher than unity, the effects of convective acceleration in such situations invalidate Darcy's law (Silberman, 1965).

Analysis of data on gravel size, permeability, and hydraulic gradient from the Carmen-Smith spawning channel,¹ and Jones Creek, Alaska, spawning channels, McNary, Priest Rapids, and Robertson Creek,² and my data from Sashin Creek, Alaska, indicates that intragravel flow is of the linear laminar type and, therefore, described by Darcy's law. I assume that these cases describe the usual conditions in salmon spawning beds and that Darcy's law is generally applicable in the description of intragravel flow.

For situations in which the Reynolds numbers are less than unity, the velocity of laminar seepage

flow within a porous medium, v , is related to the pressure gradient, $\Delta P/L$ by

$$v = -k \frac{g_c}{\mu} \frac{\Delta P}{L} \quad (1)$$

This relation is termed Darcy's law, but rather than a law, it is actually an equation which defines k , the "specific permeability," or just "permeability." In equation (1), μ is the liquid viscosity, and g_c is the constant of Newton's second law, introduced to make the equation dimensionally correct (g_c equals 1 g.-cm./dyne-sec.² in centimeter-gram-second units).

The value of ΔP can be calculated by the relation $\Delta P = \rho \frac{g}{g_c} \Delta h$, where ρ is liquid density, Δh is head loss over the distance L , and g is acceleration due to gravity. Figure 1 illustrates the variables v , k , Δh , and L . The head loss, Δh , is shown in figure 1 by the elevations to which water rises in the piezometer tubes at opposite ends of the column of porous material.

We may extend Darcy's law to account for flow due to gravity, in addition to pressure, and write expressions for velocity in each of the three directions of a cartesian coordinate system. Ratios for $\Delta P/L$ can be replaced with the corresponding derivatives:

$$v_x = -k \frac{g_c}{\mu} \frac{\partial P}{\partial x} \quad (2a)$$

$$v_y = -k \frac{g_c}{\mu} \left(\frac{\partial P}{\partial y} + \frac{g\rho}{g_c} \right) \quad (2b)$$

$$v_z = -k \frac{g_c}{\mu} \frac{\partial P}{\partial z} \quad (2c)$$

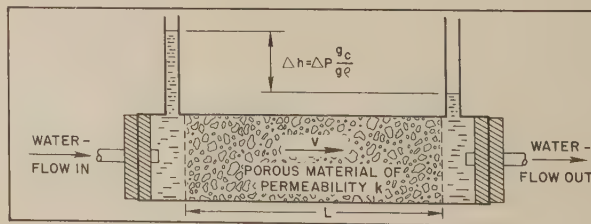


FIGURE 1.—Rectilinear waterflow through a sample of porous material showing a head loss $\Delta h = \Delta P \frac{g_c}{g\rho}$ over a distance L .

¹ Hagey, Dale W., and Robert T. Gunsolus, Progress report on the operation and evaluation of the Carmen-Smith spawning channel, 1960-64. Oregon Fish Commission, Feb. 1965, 12 pp.

² Data supplied by the Columbia Fisheries Program Office, Bureau of Commercial Fisheries, Portland, Oreg.

The coordinate system has been oriented so that the y direction is vertical and parallel to the direction of gravity. In equations (2) we assume that permeability is the same in every direction.

Equations (2) imply the single vector equation

$$\mathbf{i}v_x + \mathbf{j}v_y + \mathbf{k}v_z = -k \frac{g_c}{\mu} \left[\mathbf{i} \frac{\partial}{\partial x} (P) + \mathbf{j} \frac{\partial}{\partial y} \left(P + \frac{\rho g y}{g_c} \right) + \mathbf{k} \frac{\partial}{\partial z} (P) \right]$$

or

$$v = -k \frac{g_c}{\mu} \nabla \left[P + \frac{\rho g y}{g_c} \right] \quad (3)$$

where ∇ is the gradient operator defined by $\nabla \equiv \mathbf{i} \frac{\partial}{\partial x} + \mathbf{j} \frac{\partial}{\partial y} + \mathbf{k} \frac{\partial}{\partial z}$ and $\mathbf{i}$, $\mathbf{j}$, and $\mathbf{k}$ are unit vectors respectively in the three mutually perpendicular directions of the distance variables x , y , and z .

For later application of Darcy's law it is convenient to define the expression $\phi \equiv \frac{g_c P}{g \rho} + y$ and re-write equation (3) as

$$v = -k \frac{\rho g}{\mu} \nabla \phi \quad (4)$$

Note that ϕ , the potential for intragravel flow, represents the total energy of intragravel water and is the sum of pressure energy and elevation energy. Kinetic energy is assumed to be negligible.

The continuity equation or equation of conservation of mass for an incompressible fluid is

$$\nabla \cdot \mathbf{v} = 0 \quad (5)$$

The substitution of Darcy's law, equation (4), into equation (5) gives

$$k \nabla^2 \phi + (\nabla k) \cdot \nabla \phi = 0 \quad (6)$$

If the permeability, k , is homogeneous or uniform (i.e., independent of position) equation (6) reduces to Laplace's equation,

$$\nabla^2 \phi = \frac{\partial^2 \phi}{\partial x^2} + \frac{\partial^2 \phi}{\partial y^2} + \frac{\partial^2 \phi}{\partial z^2} = 0 \quad (7)$$

Meaningful solutions of equation (6) or (7) cannot be found until the boundary conditions (i.e., the values of ϕ or derivatives of ϕ along the boundaries of the porous bed) are specified.

I have thus far discussed any laminar flow described by Darcy's law. Components of water-

flow within a streambed are shown in figure 2. The porous streambed, A , is considered to be a stable bed consisting of particles and having a uniform permeability, k . The ambient stream, B , is continuous and uniform. The porous streambed is bounded below by an impermeable stratum, C . Any flow, D , within the porous bed is termed intragravel flow and is characterized by a velocity vector, $\mathbf{v}$. Any flow across the upper boundary of the bed is termed interchange. An upward interchange from the bed to the stream is upwelling, F ; a downward interchange is downwelling, E .

The above conditions of uniform permeability and an impermeable stratum, for which equation (7) applies, characterize most manmade spawning channels. The permeability of natural streambeds usually decreases with depth, and flow is described by equation (6). Where permeability varies with depth, one may measure permeability at several depths and assign an appropriate permeability function, $k(y)$.

Equation (6) or equation (7) for uniform permeability characterizes all laminar flow through porous materials; the boundary conditions distinguish particular seepage situations. Our consideration of intragravel flow is limited to a two-dimensional system for which four boundary conditions must be specified about a bed of finite dimensions. An infinitely long bed requires specification of two boundary conditions. Because there is no flow across the lower boundary of the porous bed, the component of waterflow normal to the boundary at the boundary is 0 and

$$\left. \frac{\partial \phi}{\partial n} \right|_{\text{boundary}, y_2(x)=0} \quad (8a)$$

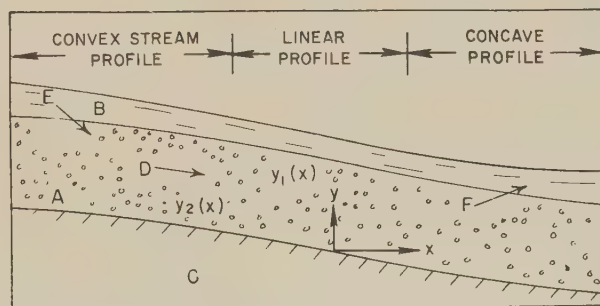


FIGURE 2.—Description of terms and properties relating to waterflow within a streambed. A , porous bed; B , ambient stream; C , impermeable stratum; D , intragravel flow; E , downwelling; F , upwelling; y_1 , bed surface profile; y_2 , impermeable stratum profile.

where n is the direction normal to the impermeable surface.

The velocity vector at any point within a streambed is influenced by streambed geometry and boundary conditions over the length of the stream. For investigation of intragravel flow in a finite reach of stream, between $x=0$ and $x=a$, we ignore upstream and downstream conditions. The boundary conditions $\phi(0,y)$ and $\phi(a,y)$ depend upon conditions over all the streambed. Since $\phi(x, y_1(x))$, hereafter denoted by $\phi(x)$, is unknown outside of $0 \leq x \leq a$, it is necessary to assign reasonable estimates of ϕ along the upstream and downstream boundaries of the isolated region. Accordingly, in isolating a region of streambed of depth b between $x=0$ and $x=a$, I specify the boundary conditions $\phi(0,y)$ and $\phi(a,y)$ to be constant and respectively equal to $\phi(0,b)$ and $\phi(a,b)$. The physical model is shown in figure 3(i)

$$\phi(0,y) = \phi(0,b) \quad (8b)$$

$$\phi(a,y) = \phi(a,b) \quad (8c)$$

Because of continuity of pressure across the stream-gravel interface, the potential at the upper bed boundary, $\phi[x, y_1(x)] \equiv \phi(x)$, must be equal to the potential at the bottom of the contiguous flowing stream. The problem of determining the potential along the upper boundary, $\phi(x)$, then becomes one of hydraulics.

The bottom pressure, $P(x, y_1)$, of a flowing stream is related to properties of the stream by

$$P(x, y_1) = \frac{\rho g}{g_c} d(x) + P_o + P_c(x, y_1) \quad (9)$$

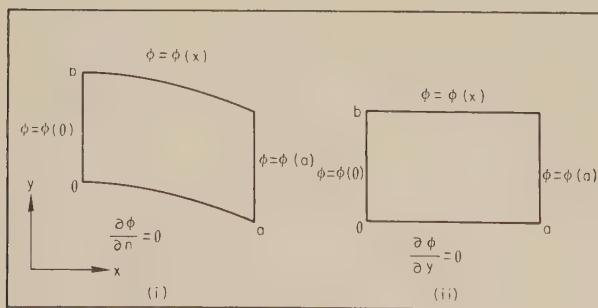


FIGURE 3.—(i) Boundary value problem representing the physical model for flow through a streambed of porous material. The shape of the region is the actual shape of the porous bed in which the upper and lower boundary curves are the topographical profiles of the bed surface and impermeable layer. (ii) Part (i) mapped into a rectangle.

in which $d(x)$ is the stream depth, P_o is atmospheric pressure, and P_c is centrifugal pressure due to stream curvature. From a stream-continuity equation, $d(x)U(x) = \text{constant}$, and the Manning flow formula,³ $U(x)d(x)^{-2/3} y'_1(x)^{-1/2} \approx \text{constant}$, where y'_1 is the hydraulic gradient and U is the average stream velocity, I find that the stream depth varies with the 0.3 power of hydraulic gradient. Considering small changes in stream gradient so that changes in $P_c(x)$ and $d(x)$ are small, it follows that changes in the right-hand side of equation (9) are small compared with changes in $y'_1(x)$ and that $g_c P / g \rho \approx \text{constant}$, from which we may approximate the potential of the upper bed boundary

$$\phi(x) = y_1(x) + \frac{g_c P(x, y_1)}{g \rho} \approx y_1(x) + \text{constant} \quad (8d)$$

The applicability of equation (8d) is limited to reaches of nearly constant stream depth (see footnote 3). Because the average velocity of streamflow is several orders of magnitude greater than the velocity of intragravel flow, the influence of interchange on stream discharge is negligible.

Equation (6) or equation (7) for uniform permeability and the equations for the four boundary conditions (8a–8d) complete the boundary value problem. Figure 3(i) depicts the model that is considered for particular solutions. Solution of the boundary value problem is facilitated by assuming the bed to be of constant depth, b (so that $y_1 = y_2 + b$ (fig. 2)) and by mapping the irregularly bounded region into a rectangle, as in figure 3(ii). The error introduced is negligible because, over short distances (e.g., less than 10 m.), natural streambeds commonly have almost constant depth and are nearly horizontal. Boundary potentials are unchanged by formation of a rectangle.

Analytical solutions of the boundary value problem describing intragravel flow usually involve the use of infinite series, i.e., are of open form. Two simple closed-form solutions arise in the methods used here to solve the problem.

1. A potential $\phi(x) = \phi(0) - \phi(0)x/a + p \sin(\pi x/a)$ in which p is an arbitrary constant holds in a curved streambed surface profile for $0 < x < a$. According to equation (8d) the profile has a

³ This form of the Manning equation implies that the stream hydraulic radius is equal to $d(x)$, that bed roughness is constant in the direction of flow, and that the stream energy gradient is parallel to the streambed surface.

negative slope and is convex if $0 < p \leq \phi(0)/\pi$, and concave if $0 > p \geq -\phi(0)/\pi$ (See figure 2). The solution to the boundary value problem equation (8a-d) for this surface potential and a bed of uniform permeability is

$$\phi(x,y) = p \frac{\cosh(\pi y/a)}{\cosh(\pi b/a)} \sin(\pi x/a) + \phi(0) - \frac{\phi(0)x}{a} \quad (10)$$

If we define interchange as the vertical (y -directed) component of intragravel flow at the streambed surface (fig. 2) the exact magnitude of interchange is given by

$$\mathbf{v}_y|_{y=b} = -k \frac{\rho g}{\mu} \frac{\partial \phi}{\partial y} \mathbf{j}|_{y=b} \quad (11)$$

For the example at hand the interchange velocity is

$$\mathbf{v}_y|_{y=b} = -k \frac{\rho g}{\mu} \frac{\pi p}{a} \tanh \frac{\pi b}{a} \sin \frac{\pi x}{a} \mathbf{j} \quad (12)$$

This example shows that the direction of interchange depends on the shape of the streambed surface. A convex streambed profile for which p is positive induces a negative interchange velocity or downwelling; a concave profile for which p is negative causes upwelling.

2. Statement of the boundary value problem for an infinitely long streambed requires only equations (6), (8a), and (8d). We may solve the boundary value problem for the flow within an infinitely long streambed by the mathematics of complex variables (Weinberger, 1965, pp. 201-268). The transformation $\zeta = (\cosh Z - 1)/\sinh Z$ conformally maps an infinitely long streambed of depth $b = \pi/2$ in the Z plane into a half disk in the ζ plane. The boundary potential $\phi(x) = -q \tanh x$ for $-\infty < x < \infty$ where q is a positive dimensionless, adjustable parameter is associated with the sigmoid-shaped streambed in figure 2. The solution of the boundary value problem is $\phi(x,y) = -q \sinh x / (\cosh x + \cos y)$. From equation (11) we find the interchange velocity to be

$$\mathbf{v}_y|_{y=b} = kq \frac{\rho g}{\mu} \frac{\sinh x}{\cosh^2 x} \mathbf{j} \quad (13)$$

As in the previous example, downwelling takes place in a convex streambed profile ($-\infty < x < 0$) and upwelling in a concave profile ($0 < x < \infty$).

ANALOG MODEL INVESTIGATION OF INTRAGRAVEL FLOW

An electrolytic-bath analog model was used to solve the boundary value problem (equations 7 and 8a-8d) for several specified boundary conditions and a streambed of uniform permeability. This technique of solving the partial differential equations of intragravel flow rests upon the analogy between Darcy's and Ohm's laws and the respective steady-state conservation equations of mass and electrical charge. An electrolytic equivalent of a streambed section with intragravel flow can be prepared by constructing a shallow tray geometrically similar to the two-dimensional porous bed. The depth of the conducting liquid at any point in the tray is proportional to the permeability at the corresponding point in the porous bed. The conducting tray walls, usually metal strips, are set at voltages proportional to the analogous hydrodynamic flow potentials or values of ϕ (Zangar, 1953, p. 24).

EQUIPMENT AND PROCEDURE

The electrolytic-bath model constructed for this investigation was a 10- by 20-cm. plexiglass tray filled to a depth of 2.5 cm. with a 0.01 normal solution of aqueous sodium chloride (fig. 4). The end walls representing constant potential (constant ϕ) surfaces were brass strips; a nonconducting strip represented a water-impermeable surface. Rheostat-controlled voltages applied separately to each of 15 electrodes along the variable-potential wall ($y=b$) provided an approximation to the potential function, $\phi(x)$.

In all operations of the analog model, 10 volts of 60-cycle alternating current were impressed

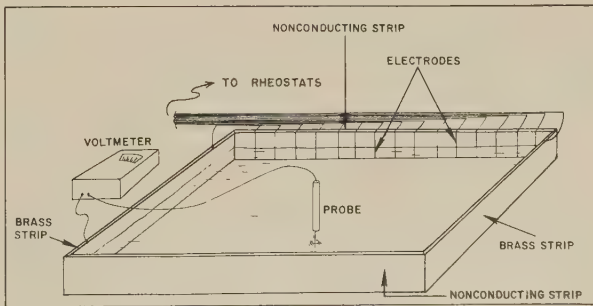


FIGURE 4.—Electrical circuits and physical layout for electrolytic-bath analog model used to investigate flow of intragravel water in a streambed.

between the brass strips; appropriate intermediate voltages were applied to the electrodes.

Solutions of the partial differential equation for different boundary conditions were obtained by tracing with a probe connected in series with a voltmeter and one tray wall along constant potential lines in the electrolyte. Results were recorded with a pantograph.

DIRECTION OF FLOW

Figures 5 through 9 represent longitudinal cross sections of a streambed: the top surface of the figure represents the upper surface of the streambed and the bottom, the impermeable stratum. The right and left ends of each figure represent arbitrary vertical planes bounding the reach of streambed considered. The lines of constant

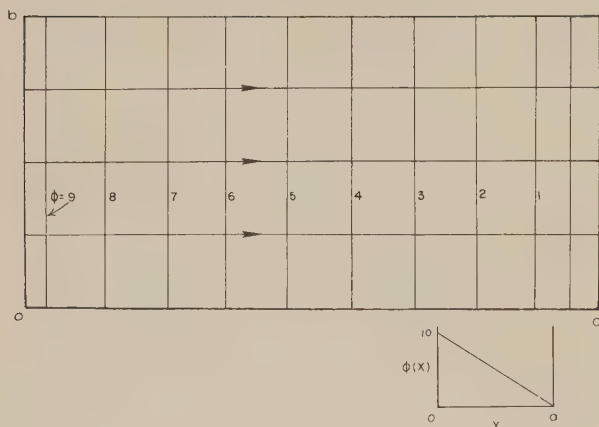


FIGURE 5.—Flow net for straight-line-surface potential $b/a = 1/2$.

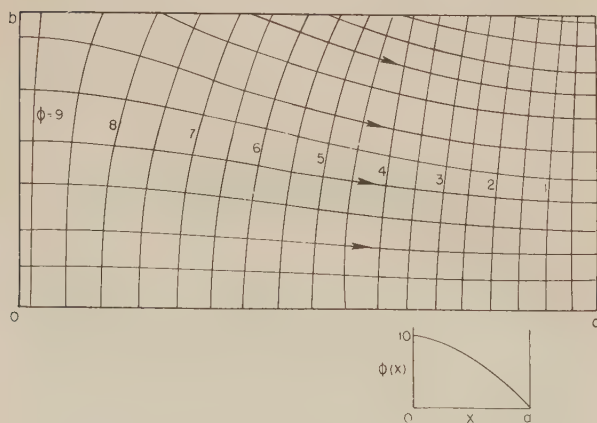


FIGURE 6.—Flow net for convex parabolic surface potential.

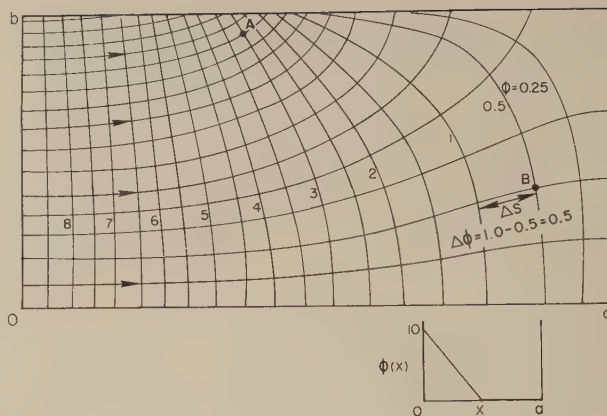


FIGURE 7.—Flow net for concave broken-line-surface potential, illustrating evaluation of Δs and $\Delta \phi$.

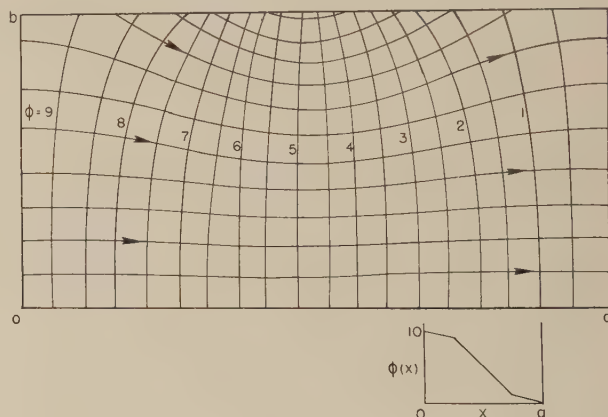


FIGURE 8.—Flow net for sigmoid surface potential.

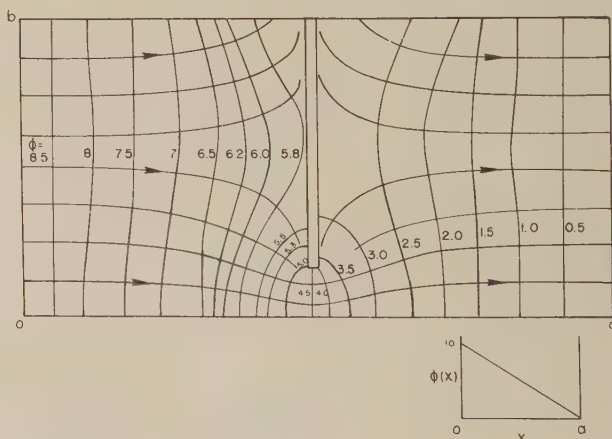


FIGURE 9.—Flow net for straight-line surface potential with impermeable intragravel barrier at $x = 0.5a$, $b/a = 1/2$.

potential, shown in the figures to be approximately vertical, were obtained from the analog model; the intragravel flow streamlines were later drawn normal to the constant potential lines to obtain a grid of "curvilinear squares" (Zangar, 1953, p. 17). Actually, the lines of constant potential shown are the analogs of the recorded lines of constant voltage, and the intragravel flow streamlines are the analogs of electrical current vectors. Figures 5, 6, 7, and 8 show the flow nets corresponding to certain of the boundary potential functions, $\phi(x)$, investigated. Figure 9 shows the effect of changed permeability on flow.

EFFECTS OF STREAMBED CHARACTERISTICS ON WATER INTERCHANGE

Accompanying each of the analog solutions shown in figures 5 through 9 is a small figure showing the function, $\phi(x)$, investigated. Since the flow potential along the open surface is approximately the elevation of the porous bed surface plus a constant, i.e., $\phi(x) = y_1(x) + \text{constant}$, each of the graphs is, in effect, a longitudinal profile of the streambed associated with the function. Figure 5 shows the pattern of intragravel flow within a streambed whose surface is straight. The profile of figure 6 may be viewed as a longitudinal convex stream section. Figure 7 illustrates the intragravel flow expected in the streambed beneath and beyond a rapids.

Figure 8 illustrates intragravel flow near a riffle between two low-gradient stream sections. This pattern of intragravel flow typifies the mechanism by which respiring salmon eggs and alevins are supplied with dissolved oxygen. Freshly oxygenated water downwells into the streambed, passes through the streambed's interior where oxygen is removed by salmon embryos or alevins, and upwells back into the stream.

The effect of placing a sheet piling in the gravel bed is shown by comparing the flow net of figure 5 with that of figure 9. Note that the streambed-surface potential, $\phi(x)$, in figure 9 is the same as that in figure 5 where, in the absence of a sheet piling, there is no interchange. The sheet piling directs intragravel flow to the surface upstream and induces downwelling downstream of the piling. The extent of interchange induced depends on the depth to which the piling is driven and the nearness of its bottom edge to an impermeable stratum.

Figures 5, 6, 7, and 8 show that the flow nets are characterized by variable directions of interchange: upwelling, downwelling, or interchange in both directions. Furthermore, the x -directed component of intragravel flow is always positive. From an analysis of many similar analog solutions and from observations in natural streams, I have found that downwelling occurs in longitudinally convex stream sections, as illustrated in figure 6. Similarly, upwelling takes place in longitudinally concave stream sections.⁴

Natural stream profiles usually contain alternate convex and concave reaches which cause alternate regions of upwelling and downwelling of stream water into and from the streambed. The penetration depth of this interchange flow depends on streambed geometry, e.g., the amount of curvature of the bed surface and depth of the streambed. In artificial spawning channels of uniform depth of streambed and uniform permeability, the bed surface is often groomed to an almost flat surface, and almost no potential exists for interchange. The movement of oxygen-rich water into the streambed must be by mechanisms other than normal water interchange, such as mechanical dispersion.

The flow nets of figures 5 through 9 show relative magnitude as well as direction of intragravel flow. Velocity of intragravel flow varies inversely with distance between lines of flow potential. When the lines are closely spaced, as at point A in figure 7, intragravel flow velocity is high. Widely spaced lines, as at point B in figure 7, show a low velocity of intragravel flow. Numerical values of velocity are calculated from equation (4), through use of a value of

$$|\nabla\phi| \simeq \frac{\Delta\phi}{\Delta s}$$

taken from the flow net as illustrated in figure 7 ($\Delta\phi$ is read as "the change in ϕ "). The symbol s is the distance variable along a streamline. The streamlines indicate the direction of intragravel flow.

⁴ A. C. Cooper (1965), in a study of intragravel flow in salmon redds, showed results of intragravel backflow, $v_x < 0$, and upwelling beneath a convex streambed surface. For this geometry the small radius of curvature of the streambed surface does not allow the approximation of equation (8d), and the boundary condition at the streambed surface, $\phi(x)$, must be obtained by a more rigorous approach. The geometry of Cooper's model studies suggests counter pressure gradients at the streambed surface and reaches of strongly variable streambed depth in the direction of flow. Such conditions would account for an upstream flow of intragravel water.

Errors in the technique included resistance heating of the electrolyte and polarization of the electrodes. The effect of polarization is shown where the potential gradient near the equipotential wall at $x=0$ is particularly steep.

The solutions of figures 5 through 9 for $b/a=1/2$ are not affine solutions; that is, they cannot be "stretched out" to describe exactly the intragravel flow in porous beds of different depth-length ratios. The flow nets shown, however, bear resemblance to and have the same general dependence on boundary-potential shape as rectangular beds of any depth-length ratio.

We have seen that for uniform permeability and constant bed depth, direction and magnitude of interchange depend upon configuration of the streambed surface. Direction and magnitude of interchange vary as well with longitudinal variations in depth and permeability of the streambed.

Consider the streambed section of figure 10. For this section the intragravel-flow streamlines will have a form somewhat like that shown in section C. Assume that all streamlines are parallel to the lower bed boundary, as in B of figure 10, and that water leaves or enters the streambed by a y -directed velocity (interchange) concentrated at the upper bed boundary, $y=b$ (see Lubyako, 1956, for discussion of this assumption). By a mass balance about the lamina of depth, b , width, w , and thickness, Δx , shown in A of figure 10,

$$\rho b w v_x|_x - \rho b w v_x|_{x+\Delta x} = v_y w \Delta x \rho. \quad (14)$$

In the limit as Δx approaches zero, the interchange, $v_y|_{y=b}$, is given by

$$v_y \Big|_{y=b} = -\frac{d}{dx}(bv_x). \quad (15)$$

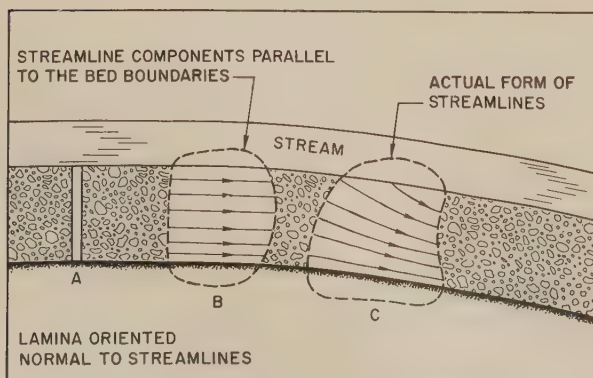


FIGURE 10.—Idealized concept of intragravel flow in a streambed.

Combining equation (15) with Darcy's law for the x -directed component of velocity

$$v_x = -k \frac{\rho g}{\mu} \frac{d\phi}{dx}, \quad (16)$$

and equation (8d) yields

$$v_y \Big|_{y=b} = -\frac{\rho g}{\mu} \frac{d}{dx} \left(b k \frac{dy}{dx} \right). \quad (17)$$

Equation (17) agrees with the analytical and analog results for interchange direction. For constant bed depth, d , and permeability, k ,

$$v_y \Big|_{y=b} = \frac{\rho g}{\mu} b k \frac{d^2 y_1}{dx^2}. \quad (18)$$

For a longitudinally convex streambed surface, $d^2 y_1/dx^2$ is negative, and equation (18) implies a downwelling. Conversely, equation (18) indicates upwelling with a concave streambed surface.

From equation (17) I have summarized in table 1 the dependence of interchange upon streambed permeability and geometry, both of which may be regulated to control the direction of interchange. Assuming that the permeability of a streambed may be increased by removing fine materials (Krumbein and Monk, 1942; McNeil and Ahnell, 1964) or that the effective gravel-bed depth (i.e., depth to which intragravel flow can occur) may be increased by removing fine particles from lower strata, it should be possible to create the interchange patterns shown in figures 11, 12, and 13. It should also be possible to control direction and amount of interchange in salmon spawning areas by varying the streambed-surface profile (fig. 14).

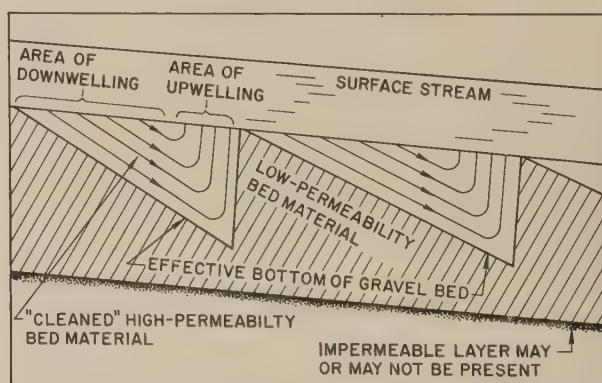


FIGURE 11.—Interchange induced by variation of depth of the streambed.

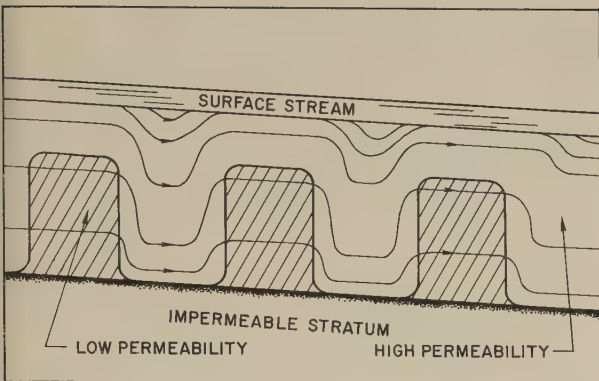


FIGURE 12.—Interchange induced by creating adjacent regions of high and low permeability.

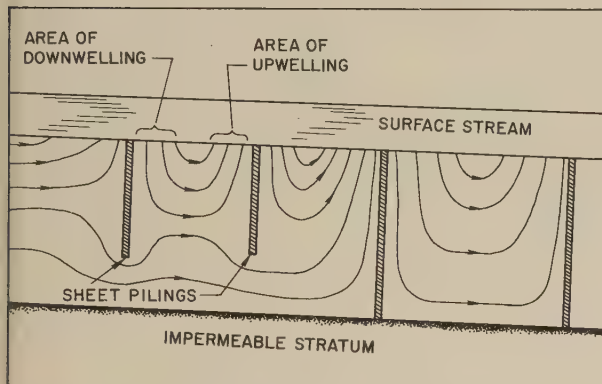


FIGURE 13.—Interchange induced by sheet pilings.

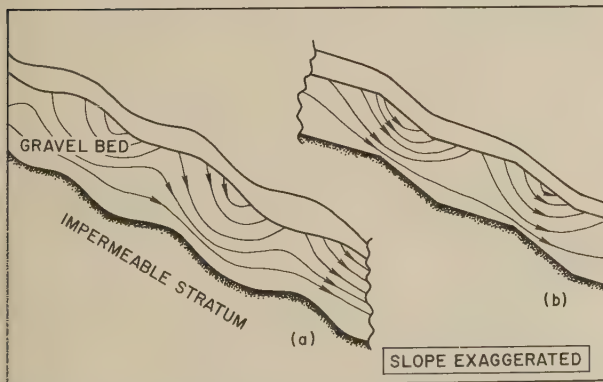


FIGURE 14.—Interchange established in streambeds by shaping the gravel bed into (a) a rounded profile and (b) an angular profile.

CONCLUSIONS

A constantly changing supply of well-oxygenated water is required in salmon spawning beds for proper survival, growth, and development of salmon embryos and alevins. Interchange between stream and intragravel water is essential for the delivery of adequate dissolved oxygen to pre-emergent fish. Knowledge of the factors that control interchange aids in understanding mortality factors and in developing means of increasing production of salmon fry from spawning beds.

TABLE 1.—Summary of effects of permeability, depth, and surface profile of streambed on interchange

Streambed characteristics	Causes upwelling	Causes downwelling	Illustrated in figure(s)
Bed depth, $b(x)$ ----	Decreasing in the direction of flow.	Increasing in the direction of flow.	11.
Permeability, $k(x)$ -----	do-----	do-----	12, 13.
Bed-surface profile, $y_1(x)$ (see fig. 2).	Concave-----	Convex-----	6, 7, 8.

Waterflow within a spawning bed can be described by Darcy's law and an equation of conservation of mass for an incompressible fluid. The potential causing intragravel flow,

$$\phi = y + g_e P / \rho g,$$

is the solution of the equation resulting from combination of Darcy's law and the mass conservation equation.

The potential along the stream-streambed boundary is described approximately by

$$\phi(x) = y_1(x) + \text{constant},$$

where $y_1(x)$ describes the profile of the streambed surface.

Interchange is controlled by the shape of the longitudinal profile of the streambed and longitudinal gradients of permeability and depth of the gravel bed according to the approximation

$$v_y \sim \frac{Pg}{\mu} \frac{d}{dx} \left(kb \frac{dy_1}{dx} \right).$$

A concave streambed surface induces upwelling, and a convex surface induces downwelling. Increasing permeability of the streambed (measured in the direction of waterflow) induces downwelling, and decreasing permeability induces upwelling. Increasing bed depth (measured in

the direction of waterflow) causes downwelling, and decreasing bed depth causes upwelling. The relation between direction of interchange and the shape of the streambed surface profile of the spawning bed was tested with an electrolytic-bath analog model and found to be correct.

The results of this work clearly demonstrate that the direction and magnitude of interchange in salmon spawning beds can be controlled by simple alteration of one or more of the three characteristics: (1) the surface profile of the bed, (2) the bed depth, and (3) the bed permeability. Selective removal of fine particles from "patches" of spawning gravel or the driving of impermeable sheet pilings could, for example, increase interchange and the amount of dissolved oxygen delivered to eggs and alevins.

NOTATION

Symbol	Notation	Units (Length, force, mass, time)
a	Length of reach of streambed.	L
b	Depth of streambed.	L
c_1, c_2	Constants of Ergun's equation.	FtL ⁻⁴
d	Stream depth.	L
g	Acceleration due to gravity.	Lt ⁻²
g_c	Newton's law constant, defined by force = $\frac{1}{g_c}$ mass $\times$ acceleration.	MLF ⁻¹ t ⁻²
Δh	Head loss.	L
i	Unit vector in x direction.	
j	Unit vector in y direction.	
k	Unit vector in z direction.	
k	Permeability, a function of (x, y, z).	L ²
L	Length of permeameter.	L
n	Distance variable in direction normal to a surface.	L
N_{Re}	Reynold's number based on particle diameter.	
p	Parameter for adjusting boundary potential in equation (10).	Dimensionless
P	Pressure.	FL ⁻²
q	A positive adjustable parameter, (equation (13)).	Dimensionless
s	Distance variable along a streamline.	L
$U(x)$	Average stream velocity.	Lt ⁻¹
v	Seepage velocity.	Lt ⁻¹
w	Width of streambed.	L
x, y, z	Distance variables along axes.	L
y_1	Elevation of streambed surface.	L

NOTATION—Continued

Symbol	Notation	Units (Length, force, mass, time)
y_2	Elevation of surface of impermeable stratum.	L
Z	Complex variable = $x + \sqrt{-1} y$.	
ζ	Complex variable in image plane.	
μ	Liquid viscosity.	ML ⁻¹ t ⁻¹
ρ	Water density.	ML ⁻³
ϕ	Potential for intragravel flow.	L
$\phi(x)$	Potential at bed surface = $\phi[x, y, (x)]$.	L
	$\nabla = i \frac{\partial}{\partial x} + j \frac{\partial}{\partial y} + k \frac{\partial}{\partial z}$, the gradient operator.	L ⁻¹
	$\nabla^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} + \frac{\partial^2}{\partial z^2}$, the laplacian operator.	L ⁻²

NOTES

Vectors are denoted by boldface letters, e.g., $\mathbf{v}$ is a velocity vector
 $\equiv$ is read as "is defined as"
 $\simeq$ is read as "approximately equal to"
 Δ is read as "the change in"
A vertical bar is read as "evaluated at," e.g., $|_{y=b}$
= "evaluated at $y=b$ "
 $\propto$ is read as "is proportional to"

ACKNOWLEDGMENTS

Alvin G. Anderson of the University of Minnesota provided guidance in the mathematical and experimental studies, and William J. McNeil, formerly of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, gave personal interest, assistance, and suggestions.

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MORTALITY RATES IN POPULATIONS OF PINK SHRIMP, *PENAEUS DUORARUM*, ON THE SANIBEL AND TORTUGAS GROUNDS, FLORIDA¹

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ABSTRACT

Mark-recovery experiments were made to obtain estimates of fishing and natural mortalities as a portion of studies related to the life history of commercial shrimps in the Gulf of Mexico. In two experiments, groups of pink shrimp were injected with biological stains and released into the Sanibel and Tortugas fisheries off the southwest coast of Florida. Marked shrimp were recaptured by commercial shrimp fishermen.

Mortality estimates were derived from analysis of

marked shrimp recoveries during the first 10 and 8 weeks of the Sanibel and Tortugas experiments, respectively. In the Sanibel population, fishing mortality was estimated to have been 6.8 percent for each 2-week period, and all other losses in the population were 14.8 percent; for the Tortugas population, fishing mortality was estimated to have been 13.1 percent for each 2-week period, and all other losses 19.7 percent.

In the past 3 decades, biologists have probed at various aspects of the life histories of commercial shrimps in the Gulf of Mexico. Recently, large-scale, mark-recovery experiments were made to estimate rates of fishing and natural mortalities in shrimp populations. A mark-recovery experiment, in which biological stains were the marking agent, was undertaken on the Tortugas pink shrimp (*Penaeus duorarum*) trawling grounds west of Key West, Fla., in September 1961. Development of an appropriate recovery system brought return of 21.1 percent of the marked shrimp. These shrimp were in commercial catches and returned by fishermen at shrimp landing ports. Analysis of data produced estimates of the rate of fishing and natural mortality in the Tortugas pink shrimp population (Kutkuhn, 1966). Two similar experiments were carried out in south Florida waters in 1962 and 1963. Emphasis was placed on obtaining a complete tabulation of fishing effort and recovering a high percentage of the marked shrimp that

were recaptured by commercial gear. One experiment was on the Sanibel grounds south of Sanibel Island, and the other on the Tortugas grounds (fig. 1). These two experiments form the basis of this report.

THE SANIBEL AND TORTUGAS FISHERIES

In both fisheries, trawling gear is similar to that used elsewhere in the Gulf of Mexico (Bullis, 1951). Trawling is at night because pink shrimp usually remain buried during the day. Other species of penaeid shrimp in the catches are of minor commercial importance.

The area known as the Sanibel grounds comprises about 2,000 km.² (600 square nautical miles) of trawlable bottom in two sections south and northwest of Sanibel Island, Fla. Most fishing is on the southern portion of the grounds between the 11- and 18-m. depths. The fishery began in 1954 and has produced about 272,000 kg. (600,000 pounds) (tails) of pink shrimp annually. Peak catches are made from March through May each year when 35 to 90 vessels participate in the

¹ Contribution No. 229, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas 77552.

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FIGURE 1.—Geographic location of the Sanibel and Tortugas pink shrimp trawling grounds.

fishery. A few vessels trawl in the area throughout the year. Catches are landed at Fort Myers, Fort Myers Beach, Punta Gorda, Placida, or Naples, Fla.

The Tortugas grounds comprise about 10,000 km.² (3,000 square nautical miles) of trawlable bottom west of Key West, Fla. Most fishing is between the 18- and 55-m. depths. The fishery began in 1950 and has produced about 5,442,000 kg. (tails) of pink shrimp annually. Peak catches occur from October through March each year, and 300 to 500 vessels participate in the fishery (Iversen and Idyll, 1959). Some trawling occurs on the Tortugas grounds throughout the year. Catches are landed at Key West, Marathon,

Everglades, Fort Myers, Fort Myers Beach, or Tampa, Fla.

DATA REQUIREMENTS AND DESIGN OF EXPERIMENTS

To obtain the information required to estimate mortality rates, a group of animals is drawn from the standing crop, marked, and returned to the former environment. We assume that subsequent observations of the marked group are applicable to the population of which the group is believed to be part. Requirements for a successful experiment are that: (1) the experimental animals either are unaffected by the capture-mark-release process, or the effect is accurately measured and

considered in the subsequent analyses; (2) accurate records are obtained of the numbers, dates, and locations of recaptures; and (3) a comprehensive tabulation is obtained of fishing effort in the area where the experimental group is available.

Experiments reported by Costello and Allen (1962) and Zein-Eldin and Klima (1965) indicate marking with biological dyes has little effect on the individual shrimp. Experience gained during earlier work (Costello and Allen, 1966) allowed the capture-release phases to be carried out with negligible injury to the live animals.

Personnel stationed at principal landing ports obtained recovery information on marked shrimp from fishermen and packing plant workers. In addition, they interviewed shrimp-boat captains to determine the time, location, and extent of fishing effort. We have a record of fishing effort for all shrimp vessels trawling in the Sanibel area. We have information on 77 percent of the shrimp vessels fishing the Tortugas grounds; and from these data we have estimated the effort that applied to the area containing marked shrimp.

FIELD OPERATIONS

To arouse their interest in the experiments, shrimp fishermen were contacted individually before the release of marked pink shrimp on the Sanibel and Tortugas grounds. A reward of \$2.00 was offered for return of each marked shrimp.

In both areas, the Bureau of Commercial Fisheries chartered vessel *Silver Bay* captured shrimp and served as a platform for marking. Shrimp captured on the Sanibel grounds March 19 to 22, 1962, were stain-marked by injection of a 0.5 percent solution of fast green FCF, and 2,496 individuals were released at 26 randomly selected sites in the trawling area (fig. 2). Shrimp captured on the Tortugas grounds December 8 to 15, 1962, were stain-marked with a 0.25 percent solution of Trypan blue, and 2,350 individuals were released at 16 randomly selected sites in an area being fished by most of the fleet at that time (fig. 2).

Size compositions of marked shrimp released in both experiments, as determined from samples of marked shrimp ready for release, are shown in figures 3 and 4.

Adult pink shrimp, usually benthic, are particularly vulnerable to predation in the upper

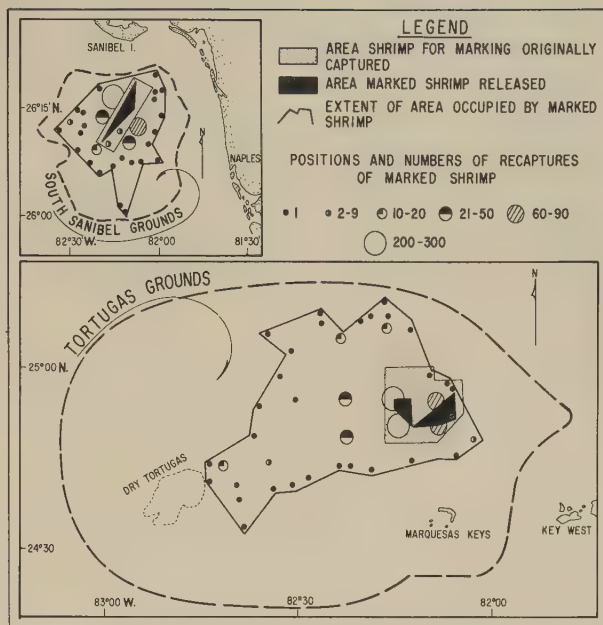


FIGURE 2.—Capture, release, and recapture areas of marked pink shrimp on the south Sanibel and the Tortugas grounds.

water layers, so an underwater release device described by Costello (1964) was used to lower and release marked shrimp near the bottom.

On the Sanibel grounds, 563 marked shrimp or 22.5 percent of the experimental population had been recovered by August 30, 1962. On the Tortugas grounds, 784 marked shrimp or 33.3 percent of those released had been recovered by March 29, 1963.

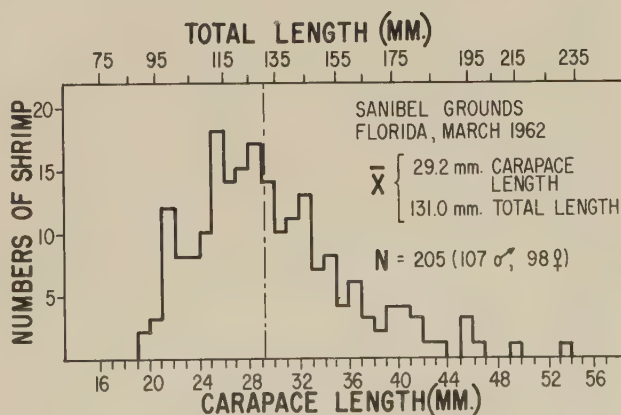


FIGURE 3.—Size composition of a random sample from the marked pink shrimp released on the south Sanibel grounds.

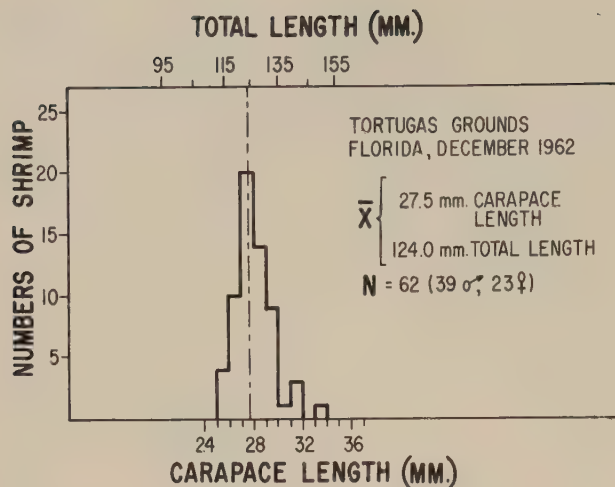


FIGURE 4.—Size composition of a random sample from the marked pink shrimp released on the Tortugas grounds.

DISPERSION OF THE MARKED SHRIMP

On both fishing grounds, plots of the positions of release and recapture of marked shrimp showed that: (1) some marked shrimp dispersed following release and (2) others remained within the immediate area of release for at least 10 weeks.

We used the release and recapture positions in both experiments to define the areas containing the marked shrimp. The outermost positions where marked shrimp were released were plotted and joined to enclose the original areas occupied; as recoveries were received, the outermost recapture positions were joined to delineate the expanding areas occupied. Definitions of the successive areas occupied were obtained with accumulation of several days' recoveries. The location of fishing effort was best established within an area from information compiled for 2-week intervals. For this reason, we selected 2-week intervals as most satisfactory.

Dispersion of marked shrimp from the original release areas proceeded at varying rates (figs. 5 and 6). Movements of the experimental group at Sanibel were generally toward the west and southwest. At Tortugas, dispersion was to the west and northwest. The outlined areas achieved midway between the first and last day of each succeeding 2-week period were selected as best descriptive of the average situation in the periods. At Tortugas, for example, the area occupied by marked shrimp at the midpoint of the first 2-week period after re-

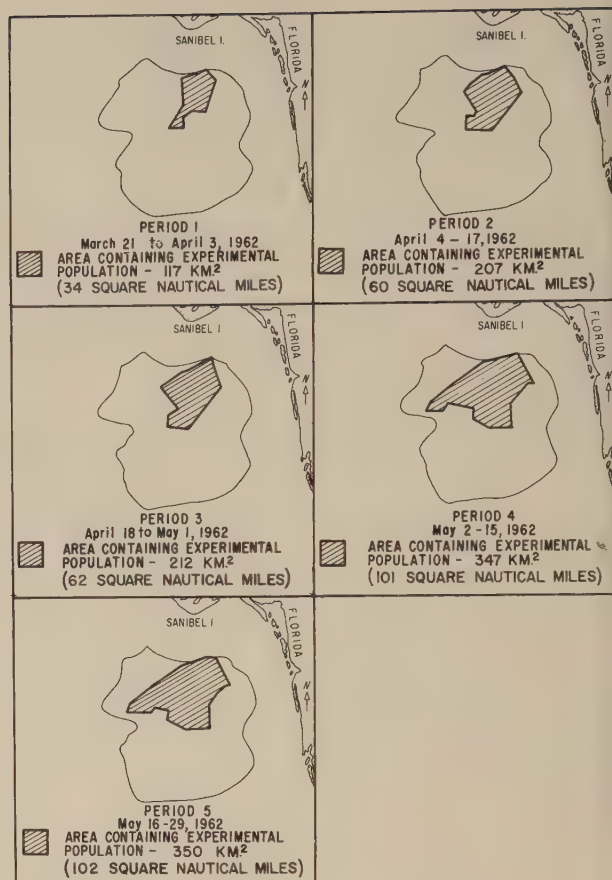


FIGURE 5.—South Sanibel grounds. Area occupied by the population of marked pink shrimp in successive 2-week periods, as determined from recapture locations.

lease was 961 km.² (280 square nautical miles). The area occupied by marked shrimp any day of that 2-week period was considered, therefore, to be 961 km.² (fig. 6). The outlines shown (figs. 5 and 6) and information from interviews on the location of fishing vessels enabled us to separate fishing effort expended in the area containing the experimental group of marked shrimp from total fishing effort on the grounds. During Period 1, in the Sanibel experiment, for example, the total effort expended on the grounds on March 31, 1962, was 16 boat-nights; the effort applicable to the experimental population was 6 boat-nights (table 1).

Description of the expanding area occupied by the marked shrimp permitted a refinement of the original data. For each 2-week period, a factor based on the relative size of the original area and the expanded area was computed. This factor

TABLE 1.—Fishing effort and recoveries of stain-marked shrimp, south Sanibel grounds, March 21 to May 29, 1962

Date	Total effort	Effort applicable to experimental population	Area containing experimental population	Factor	Fishing intensity [effort per unit area, i.e., boat-nights per 117 km. ² (34 square nautical miles)]	Recoveries
<i>Period 1</i>	<i>Boat-nights</i>	<i>Boat-nights</i>	<i>Km.²</i>			<i>Number</i>
March 21	4	4	117	1.00	4.00	1
22	2	2	117	1.00	2.00	1
23	1	0	117	1.00	.00	0
24	0	0	117	1.00	.00	0
25	0	0	117	1.00	.00	0
26	0	0	117	1.00	.00	0
27	1	1	117	1.00	1.00	11
28	5	4	117	1.00	4.00	20
29	16	6	117	1.00	6.00	29
30	17	8	117	1.00	8.00	29
31	16	6	117	1.00	6.00	13
April 1	16	6	117	1.00	6.00	31
2	6	3	117	1.00	3.00	0
3	8	4	117	1.00	4.00	0
<i>Period 2</i>						
April 4	8	6	207	0.567	3.40	4
5	7	5	207	.567	2.84	3
6	5	3	207	.567	1.70	0
7	6	3	207	.567	1.70	2
8	12	9	207	.567	5.10	37
9	13	9	207	.567	5.10	43
10	17	11	207	.567	6.24	16
11	16	10	207	.567	5.67	29
12	13	9	207	.567	5.10	27
13	10	7	207	.567	3.97	0
14	2	1	207	.567	.57	2
15	3	2	207	.567	1.13	2
16	0	0	207	.567	.00	0
17	0	0	207	.567	.00	0
<i>Period 3</i>						
April 18	3	2	212	0.548	1.10	3
19	2	1	212	.548	.55	0
20	0	0	212	.548	.00	0
21	0	0	212	.548	.00	0
22	1	0	212	.548	.00	0
23	6	4	212	.548	2.19	0
24	6	4	212	.548	2.19	5
25	15	11	212	.548	6.03	14
26	17	13	212	.548	7.12	21
27	19	10	212	.548	5.48	5
28	15	9	212	.548	4.93	8
29	16	9	212	.548	4.93	1
30	17	9	212	.548	4.93	5
May 1	12	8	212	.548	4.38	5
<i>Period 4</i>						
May 2	13	8	347	0.337	2.70	3
3	7	4	347	.337	1.35	3
4	11	8	347	.337	2.70	4
5	12	11	347	.337	3.71	13
6	14	11	347	.337	3.71	9
7	13	13	347	.337	4.38	10
8	16	15	347	.337	5.06	5
9	19	19	347	.337	6.40	5
10	17	17	347	.337	5.73	11
11	17	18	347	.337	6.07	6
12	16	16	347	.337	5.39	6
13	16	16	347	.337	5.39	4
14	7	7	347	.337	2.36	3
15	1	1	347	.337	.33	0
<i>Period 5</i>						
May 16	1	1	350	0.333	0.33	0
17	1	1	350	.333	.33	0
18	1	1	350	.333	.33	0
19	4	4	350	.333	1.33	0
20	6	6	350	.333	2.00	0
21	10	10	350	.333	3.33	1
22	12	12	350	.333	4.00	16
23	21	11	350	.333	3.66	15
24	11	11	350	.333	3.66	2
25	10	11	350	.333	3.66	7
26	12	12	350	.333	4.00	2
27	15	15	350	.333	5.00	11
28	16	14	350	.333	4.66	4
29	20	19	350	.333	6.33	8

allowed measures of fishing effort to be converted to fishing intensity, i.e., fishing effort per unit area, the form required for subsequent analyses (tables 1 and 2).

ASSUMPTIONS AND JUSTIFICATIONS IN THE ESTIMATION OF MORTALITY

Any analytical approach to estimate mortality from mark-recapture data requires certain assumptions. Those we made are listed below followed by the evidence available to justify each.

Assumption 1:

Negligible losses of marked shrimp due to marking, handling at release, or to loss of marks after release.

Justification:

Experiments on survival of shrimp reported by Costello and Allen (1962) indicate that stain-marked shrimp have almost the same mortality as unmarked shrimp even in the presence of predators. Evidence of the longevity of stain marks (Dawson, 1957) excludes the likelihood that the marks fade or are lost over the period of the present experiments. Shrimp were examined individually before release to be certain that marks were distinct.

TABLE 2.—Fishing effort and recoveries of stain-marked shrimp, Tortugas grounds, December 14, 1962 to February 7, 1963

Date	Total effort	Effort applicable to experimental population	Area containing experimental population	Factor	Fishing intensity [effort per unit area, i.e., hours per 961 km. ² (280 square nautical miles)]	Recoveries
<i>Period 1</i>	<i>Hours</i>	<i>Hours</i>	<i>Km.²</i>			<i>Number</i>
December 14	1,466	542	961	1.00		542
15	3,025	1,376	961	1.00		1,376
16	3,607	1,499	961	1.00		1,499
17	3,615	1,346	961	1.00		1,346
18	3,221	1,153	961	1.00		1,153
19	2,914	725	961	1.00		725
20	2,380	522	961	1.00		522
21	1,822	619	961	1.00		619
22	1,021	493	961	1.00		493
23	868	538	961	1.00		538
24	891	566	961	1.00		566
25	1,160	704	961	1.00		704
26	1,592	786	961	1.00		786
27	1,958	931	961	1.00		931
<i>Period 2</i>						
December 28	2,550	1,492	1,772	0.543		810
29	2,556	1,496	1,772	.543		812
30	1,360	830	1,772	.543		451
31	1,196	689	1,772	.543		374
January 1	1,175	713	1,772	.543		387
2	1,620	1,130	1,772	.543		613
3	2,158	1,602	1,772	.543		815
4	2,095	1,332	1,772	.543		723
5	2,607	1,787	1,772	.543		970
6	2,792	1,628	1,772	.543		884
7	1,044	545	1,772	.543		296
8	923	627	1,772	.543		340
9	1,809	1,397	1,772	.543		758
10	2,808	2,215	1,772	.543		1,202

TABLE 2.—Fishing effort and recoveries of stain-marked shrimp, Tortugas grounds, December 14, 1962 to February 7, 1963—Continued

Date	Total effort	Effort applicable to experimental population	Area containing experimental population	Factor	Fishing intensity [effort per unit area, i.e., hours per 961 km. ² (280 square nautical miles)]	Recoveries
<i>Period 3</i>	<i>Hours</i>	<i>Hours</i>	<i>Km.²</i>			<i>Number</i>
January 11....	3,209	2,432	2,162	0.444	1,080	19
12....	3,202	2,414	2,162	.444	1,072	20
13....	2,955	2,120	2,162	.444	941	11
14....	1,709	983	2,162	.444	436	8
15....	1,729	1,135	2,162	.444	504	7
16....	1,561	1,205	2,162	.444	535	6
17....	2,542	1,694	2,162	.444	752	10
18....	3,039	1,887	2,162	.444	838	17
19....	3,143	2,126	2,162	.444	944	23
20....	3,085	1,976	2,162	.444	877	10
21....	844	415	2,162	.444	184	1
22....	663	345	2,162	.444	153	0
23....	1,882	1,268	2,162	.444	563	4
24....	749	483	2,162	.444	214	1
<i>Period 4</i>						
January 25....	1,093	897	2,637 (768)	0.365	327	1
26....	2,698	2,292	2,637	.365	837	23
27....	2,973	2,390	2,637	.365	872	9
28....	1,835	1,377	2,637	.365	503	5
29....	1,617	921	2,637	.365	336	1
30....	2,782	2,116	2,637	.365	772	3
31....	3,118	2,630	2,637	.365	960	10
February 1....	3,289	2,743	2,637	.365	1,000	4
2....	3,185	2,461	2,637	.365	898	5
3....	1,843	1,291	2,637	.365	471	4
4....	580	236	2,637	.365	86	1
5....	488	238	2,637	.365	87	0
6....	773	319	2,637	.365	116	0
7....	1,095	621	2,637	.365	227	1

Assumption 2:

No losses due to predation during release.

Justification:

The experimental groups, as noted earlier, were returned to the bottom in a release box designed to avoid predation. The effectiveness of this release device had been demonstrated previously by underwater observations (Rounsefell, 1963).

Assumption 3:

Negligible loss of recaptured marked shrimp because of failure to detect them in the commercial catch or failure to report them.

Justification:

Assurance that a high percentage of recaptures were recognized and returned (recovered) was given by the following evidence:

a. Just before these experiments, most fishermen and processing-plant personnel in the area were shown samples of stain-marked shrimp.

b. Eight experiments with stain-marking had been performed recently in these areas, and most fishermen and processing-plant personnel in the Sanibel and Tortugas areas were familiar with stain-marked shrimp.

c. A reward was paid for each recovery when vessels arrived in port or as soon as marked shrimp were found in a processing plant.

d. During both experiments, marked shrimp had many chances to be recognized and returned because all shrimp were "headed" by hand. All Sanibel shrimp were headed at sea, but some Tortugas catches were headed ashore. Ordinarily, a single fisherman may remove heads from 8,000 or more shrimp in a single night. During the Sanibel experiment, fishermen, two to a boat, removed the heads from an average of only about 4,000 shrimp each night (table 3). When they handled less than their capacity, fishermen had time to examine each shrimp and recognize the marked animals. Considerably more shrimp were handled per night by Tortugas fishermen than by Sanibel fishermen. Crew members from many boats told us, however, that they spread catches of shrimp on the deck before heading so that marked shrimp might be easily noticed. Most of the total recoveries (93 percent) were recognized by fishermen at sea and removed from the catch before the return to port (Allen and Costello, 1966). Ashore, Bureau personnel daily reminded workers in processing plants to watch for marked shrimp that passed unnoticed by fishermen at sea.

e. "Planting" experiments indicated a high ratio of recoveries to recaptures. During the time marked shrimp occurred in commercial catches from the Tortugas grounds, small numbers were placed secretly in catches of whole shrimp being unloaded at shore processing plants. These shrimp were of identical size and were

TABLE 3.—Fishing effort and pink shrimp catch (individuals), south Sanibel grounds, March to May 1962¹

Period	Fishing effort	Total shrimp catch ²	Number of shrimp caught per boat-night ²
	<i>Boat-nights</i>	<i>Number</i>	<i>Average</i>
3/21-27.....	8	24,000	3,000
3/28-4/3.....	84	403,000	5,000
4/4-10.....	68	345,000	5,000
4/11-17.....	44	212,000	5,000
4/18-24.....	18	45,000	3,000
4/25-5/1.....	111	434,000	4,000
5/2-8.....	86	358,000	4,000
5/9-15.....	93	341,000	4,000
5/16-22.....	35	105,000	3,000
5/23-29.....	105	300,000	3,000
Mean catch per boat per night.....			4,000

¹ Based on 171 interviews of boats landing shrimp at Fort Myers and Fort Myers Beach. Compiled by Bureau of Commercial Fisheries Branch of Statistics.

² Rounded to the nearest thousand.

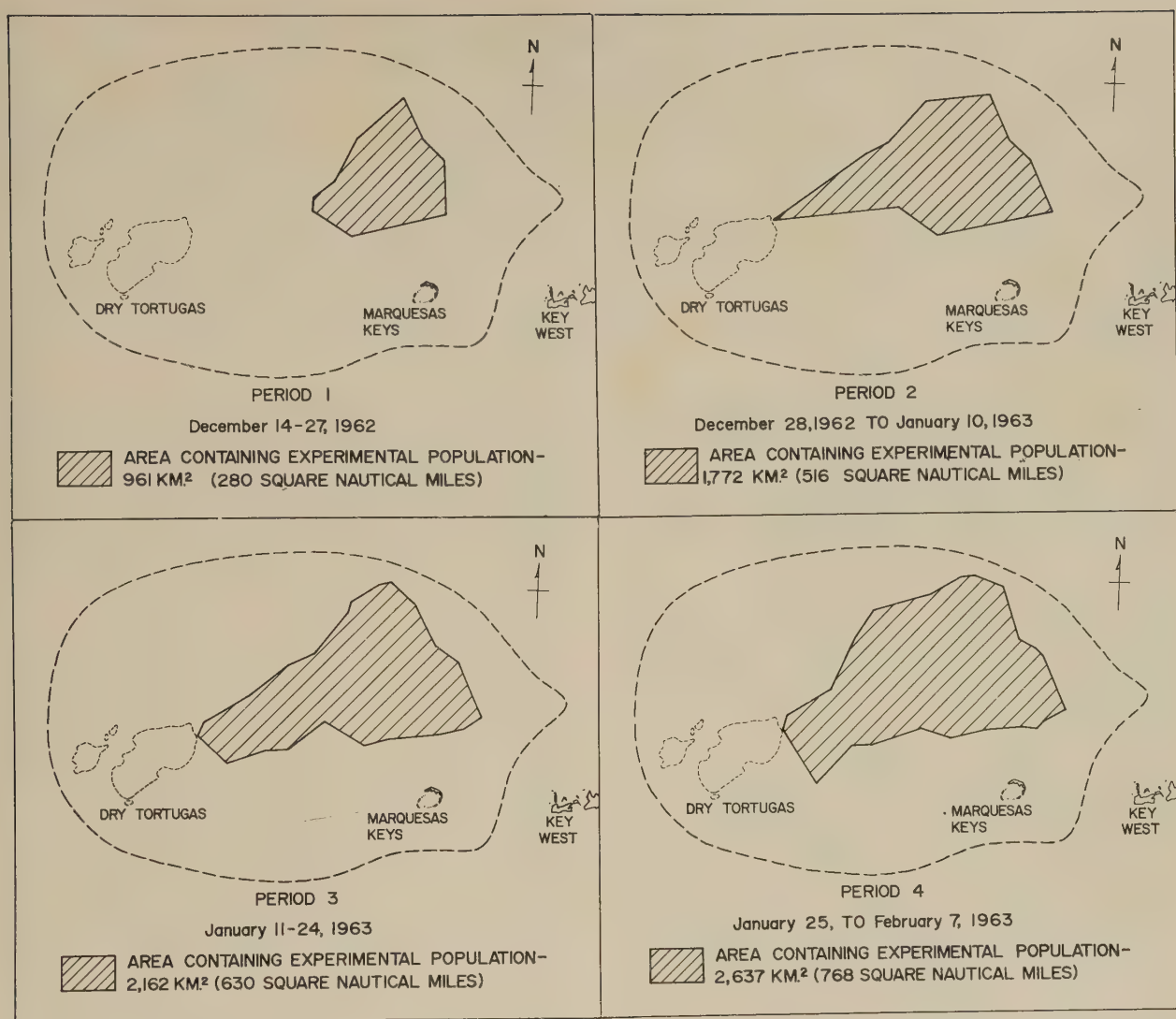


FIGURE 6.—Tortugas grounds. Area occupied by the population of marked pink shrimp in successive 2-week periods as determined from recapture locations.

stained similarly to those released on the fishing grounds. A second mark, not visible to processing plant personnel, was placed on these "planted" specimens so that we could distinguish them from genuine recoveries. Results of these and of later similar experiments indicated that 75 to 89 percent of marked shrimp which enter the shore processing plants are recovered.

We have no direct measure of the percentage of marked shrimp recovered from those headed at sea. In similar mark-recovery experiments in the northern Gulf of Mexico, however, Klima and Benigno (1965) estimated that 83 percent of re-

captured marked shrimp were recovered on shrimp boats and 14 percent were recovered in processing plants. They concluded, therefore, that only 3 percent were entirely overlooked.

Assumption 4:

If losses did occur, the ratio of undetected recaptures to recoveries did not change during the periods used in analyses.

Justification:

Field personnel concluded, from daily interviews, that interest in recovering marked shrimp aboard shrimp boats and in processing plants remained constant for at least the first 10 weeks of

both experiments. Marked shrimp were recovered over extended periods of time, but recovery and fishing-effort information collected only within the first 10 weeks following release of the marked animals was used for estimating mortality rates for the Sanibel and Tortugas experiments. The period was so restricted because recoveries of marked shrimp reflect their relative abundance in the commercial catch only as long as the interest in recovering them remains constant. The reward is a prime inducement for the return of marked shrimp. Reasonably, when the number of marked shrimp in catches drops markedly, interest wanes and an increasing percentage of recaptures may pass through the fishery unnoticed.

THEORETICAL AND BIOLOGICAL CONSIDERATIONS

Fundamental tenets in computation of mortality estimates are that the decline in numbers in an animal population follows an exponential trend, and that a constant instantaneous mortality coefficient is operative. The latter concept has been applied to many animal populations. Presumably, it may be applied to shrimp. Paulik (1963) noted the acceptability of this concept in short-term experiments, as are being considered here.

Mortality estimates are derived from mark-recovery experiments by measuring density changes in an experimental population. In this application, otter trawls used by the commercial shrimp fleet serve as sampling gear, and decreases in density are reflected in decreased catches of marked shrimp per unit fishing intensity. The average rate of loss is computed and expressed numerically as the instantaneous total mortality coefficient.

At this point, it is pertinent to offer possible explanations for the fluctuations in recoveries of marked shrimp per unit fishing intensity on the Sanibel grounds (table 4), but not on the Tortugas grounds (table 5). It appears, superficially, that decreases in the abundance of the marked shrimp from one time period to the next should be consistently reflected in decreased recaptures per unit fishing intensity. Increased recaptures of marked shrimp at a later time period appear to violate a basic premise upon which the estimate of mortality is based.

The reasons for this apparent anomaly are not entirely clear. Possible sources of bias in the interpretation of mark-recovery data may be introduced by: (1) nonuniform distribution of marked animals over the bottom and (2) inaccurate estimation of fishing effort in relation to the spatial distribution of marked animals. Such difficulties in interpretation of marking experiments were discussed by Ricker (1958).

These sources of bias, however, may not be the only causes of fluctuations in recovery of shrimp per unit fishing intensity. Allen, Delacy, and Gotshall (1960), Konstantinov (1964), Parrish, Blaxter, and Hall (1964), and others recognized that biological activities may affect the catchability of aquatic animals. Wathne (1963) and Fuss and Ogren (1966) noted variable burrowing habits of pink shrimp which may explain variations in shrimp availability to the trawl. Additionally, although pink shrimp are ordinarily benthic, we have frequently observed them in dense schools at or near the surface at night. Similar observations were reported by Burkenroad (1949), Higman (1952), Tabb, Dubrow, and Jones (1962), Iversen and Van Meter (1964), and Joyce (1965). Obviously, vertical movements of

TABLE 4.—Fishing intensity and numbers of marked shrimp recovered, south Sanibel grounds, March 1962 to May 1962

[N₀ = 2,496]

Recovery interval	Marked shrimp recovered	Applicable fishing effort	Area occupied by experimental population	Factor based on area occupied	Fishing intensity (effort per unit area)	Recoveries ¹	Natural logs of recoveries ¹
	<i>Number</i>	<i>Boat-nights</i>	<i>Km.²</i>			<i>Number</i>	
3/21-4/3	135	44	117	1.00	44.0	139.9	4.94092
4/4-4/17	165	75	207	.567	42.5	177.0	5.17615
4/18-5/1	67	80	212	.548	43.8	69.8	4.24563
5/2-5/15	82	164	347	.337	55.3	67.6	4.21361
5/16-5/29	66	128	350	.333	42.6	70.6	4.25703
5/30-8/30 ²	47						

¹ Per (mean) 45.6 boat-nights fishing intensity.

² Recoveries during this final period were not used in analysis.

TABLE 5.—*Fishing intensity and numbers of marked shrimp recovered, Tortugas grounds, December 1962 to February 1963*

[N=2,350 ¹]

Recovery interval	Marked shrimp recovery	Applicable fishing effort	Area occupied by experimental population	Factor based on area occupied	Fishing intensity (effort per unit area)	Recoveries ²	Natural logs of recoveries ³
	<i>Number</i>	<i>Thousand hours</i>	<i>Km. ²</i>			<i>Number</i>	
12/14-12/27-----	302	11.8	961	1.00	11.8	241.8	5.4881
12/28-1/10-----	213	17.4	1,772	0.543	9.4	214.1	5.3665
1/11-1/24-----	137	20.5	2,162	.444	9.1	142.2	4.9572
1/25-2/7-----	67	20.5	2,637	.365	7.5	84.4	4.4356
2/8-3/29 ³ -----	29						

¹ In analysis, this number adjusted to 2,314 for the mean release date of 12/14/62.

² Per (mean) 9,450 hours of fishing intensity.

³ Recoveries during this final period were not used in analysis.

shrimp in the water mass will affect their availability to a trawl fishing on or near the bottom.

Over short periods of time then, we may normally expect considerable variability in catches of pink shrimp (unmarked or marked) which is independent of the decrease in a population with time.

DEFINITIONS OF NOTATIONS

Notations and symbols suggested by Beverton and Holt (1957) and Holt (1960) are used in our analysis and summary. Definitions follow:

Z =Instantaneous total mortality coefficient

F =Instantaneous coefficient of mortality caused by fishing

M =Instantaneous coefficient of mortality by (natural) causes other than fishing

X =Instantaneous coefficient of other loss in marking theory, i.e., losses in the experimental population due to all causes except recapture (true natural mortality plus losses of individuals which for any reason become unavailable for recapture)²

f =Fishing intensity (fishing effort per unit area)

N_0 =Initial size of the experimental population (number in batch of marked shrimp liberated at time zero)

n =Number of marked shrimp recaptured in a given period, e.g.,

n_1 =Number in first period, n_2 =Number in second period, etc.

ANALYSIS

Variations in catch per unit fishing intensity

² As defined by Beverton and Holt (1957). Holt (1960) gave a varied meaning.

described previously do not nullify the value of this information in deriving mortality estimates. Population decreases with time during the experimental period are reflected well by these data. An analytical technique designed to yield mean instantaneous mortality coefficients, accordingly, was chosen.

The numbers of marked shrimp recaptured each 2-week period varied considerably in both experiments in response to fluctuating fishing intensity. As suggested by Kutkuhn (1966), the numbers of recoveries that accumulate each period may be corrected to unit fishing intensity and analytical methods given by Beverton and Holt (1957, pp. 185-191) applied. A factor of 45.6, the average number of boat-nights ³ of fishing intensity per 2-week period, was applied to Sanibel recoveries to convert them to a unit basis (table 4); a factor of 9,450, the average number of hours of fishing intensity per 2-week period, was used to convert the Tortugas recoveries (table 5). We recognize, however, that this method of analysis is better suited to the Tortugas experiment than to the Sanibel experiment where fishing intensity fluctuated considerably from period to period.

Lines fitted to the natural logarithms of adjusted recoveries (figs. 7 and 8) indicate that the decline in numbers of both experimental groups followed a linear trend. Regression lines have a slope equal to minus $(F+X)$ or Z . For Z , the instantaneous total mortality coefficient, the regression equations yielded values of 0.233 for Sanibel and 0.357 for Tortugas. Values of 153.4 and 121.5 (designated n_1 and n_2) were obtained by substituting appropriate units of time in the regression equation for Sanibel. These figures are

³ Sanibel fishing effort was reported to us in boat-nights rather than in hours. No valid conversion factor was available to convert boat-nights to hours; therefore, Sanibel effort was used in the form of boat-nights as originally reported.

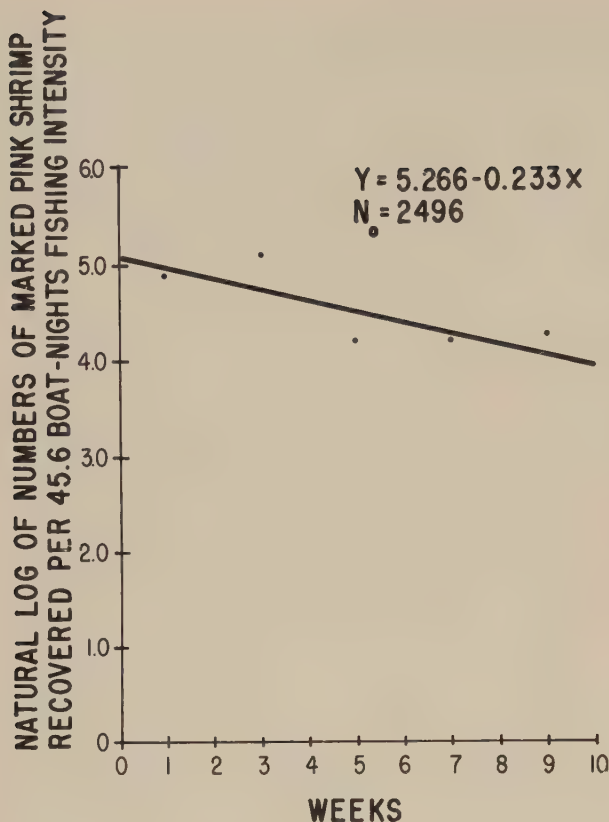


FIGURE 7.—Mortality of marked pink shrimp, south Sanibel grounds, March 21 to May 29, 1962.

the theoretical numbers of recoveries of marked shrimp that would have occurred in the first and second 2-week periods following release of the experimental population with fishing intensity constant at 45.6 boat-nights per 2-week period. For the Tortugas fishery, on the basis of 9,450 hours of fishing intensity per 2-week period, a like procedure gave values of 269.3 and 188.5 for n_1 and n_2 . With these numerical values for n_1 and n_2 , and the N_0 figures given in tables 4 and 5, we may enter the following expressions from Beverton and Holt (1957, p. 190).

$$F = \frac{\frac{n_1}{\tau} \log_e \left(\frac{n_1}{n_2} \right)}{N_0 \left(1 - \frac{n_2}{n_1} \right)}$$

$$X = \frac{1}{\tau} \left\{ \log_e \left(\frac{n_1}{n_2} \right) \right\} \left\{ 1 - \frac{n_1}{N_0 \left(1 - \frac{n_2}{n_1} \right)} \right\}$$

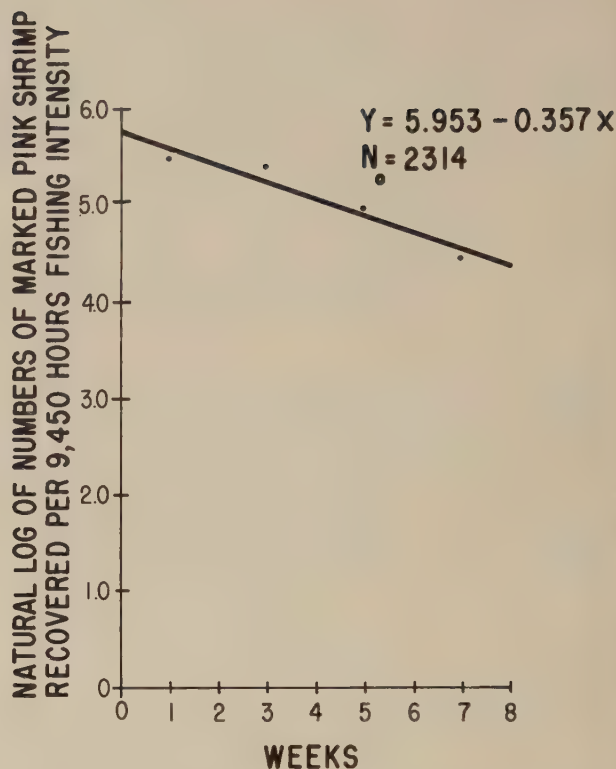


FIGURE 8.—Mortality of marked pink shrimp, Tortugas grounds, December 14, 1962, to February 7, 1963.

By application of these expressions, we divide the Z values given above into fishing mortality (F) and "other losses" components (X).

These calculations gave the following estimates:

	Mortality	Instantaneous rates	Rates (percent) per 2-week period
Sanibel.....	Fishing.....	0.0689	6.8
	Other.....	.1644	14.8
Tortugas.....	Fishing.....	.1385	13.1
	Other.....	.2185	19.7

SUMMARY

Mortality estimates for the Sanibel population have not been previously reported. For the Tortugas population, estimates derived here indicate mortality higher than was reported by Iversen (1962), but considerably lower than was calculated by Kutkuhn (1966).

In either the Sanibel or Tortugas experiment the values obtained for X (coefficient of other loss) cannot be readily accepted as estimates of

M (coefficient of true natural mortality). By definition, X includes M, together with losses from all other causes except fishing. Losses due to migration from the area of fishing, and mortality attributable to marking, handling, or the release procedure can contribute a considerable loss to the experimental group of animals. This fact must be given consideration in the use of X as an estimate of M.

Consideration of possible management implications calls for recognition that operation of trawls may have complex effects upon a resident shrimp population (Lindner, 1936). Also, cessation of trawling affects the population. The mortality estimates we have given were calculated from data assembled while a sizable fishery was in progress. The coefficient of true natural mortality may shift considerably when a regulatory measure, e.g., closure of the fishery, is applied.

F, as a function of fishing effort, fluctuates over short periods of time. The value of M also changes in response to such factors as varying predation by migratory schools of fish. The values derived here, however, for shrimp of the sizes in the experiment, may establish the approximate levels for offshore pink shrimp fisheries. These parameters, together with supplementary information and recommendations by Lindner (1966), may be used as a basis for management of the valuable Sanibel and Tortugas resources.

ACKNOWLEDGMENTS

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OCEANOGRAPHIC CONDITIONS IN THE NORTHEAST PACIFIC OCEAN AND THEIR RELATION TO THE ALBACORE FISHERY

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ABSTRACT

This paper describes initial environmental conditions encountered by albacore, *Thunnus alalunga* (Bonnaterre), in their annual entry to the region off the northwest coast of the United States, describes the physical mechanisms that produce these conditions, and indicates their influence on the highly variable number of albacore available to the fishery. The region studied extends from the coast of Oregon and Washington to long. 132° W. between lats. 41° N. and 48° N., within which the northernmost part of the American coastal fishery for albacore usually has been confined.

Upwelling, effects of runoff from land, and the excess of precipitation over evaporation produce annually recurrent patterns of distribution of variables. This recurrent aspect is used to distinguish three spatial provinces above and two provinces below the main halocline, each of which reflects the balance of processes affecting it. Variations in the distributions of variables from year to year are shown to be attributable to

changes in wind field, in fresh-water discharge from land, and in advection. These variations do not, however, obscure the basic patterns generated by dominant processes.

The distribution of available albacore over the study area is inferred to be sensitive to spatial and year-to-year differences in temperature and in salinity. Higher temperatures, produced by greater retention of heat in the surface layer of the province dominated by effects of land runoff, may give rise to greater concentrations of albacore in this province. Salinity, to which temperature is inversely related, may control the degree to which spatial temperature differences can be effective, possibly by its influence on osmotic pressure. If future investigation confirms this hypothesis, success of the fishery will be predictable from preseason information on wind field, geostrophic flow, and Columbia River discharge.

The yield of the seasonal fishery for albacore (*Thunnus alalunga*) off Oregon and Washington is characteristically variable. Within the period 1951-64, annual landings in these States ranged from 0.6 to 13.5 million pounds. Nearly all albacore landed in Oregon and Washington in 1954 and 1955 were caught south of lat. 40° N.; consequently, the northern fishery was considered to have failed completely in these years.

The region off the Oregon-Washington coast usually represents the northernmost end of the range within which commercially harvestable concentrations of albacore have been found along the North American coast. The fishery spans a shorter time interval than that to the south, perhaps because environmental conditions are tolerable to albacore for a shorter time. Fishing usually begins there in mid-July, attains a maximum effort and catch in late August and September, and largely ends by the end of October. The California fishery, by contrast, often starts a month earlier and ends a month later. Moreover, fishing intensity off Oregon and Washington is more sensitive to weather, to the price

of albacore, and to diversion from tuna trolling to salmon fishing and bottom fishing than off California. Variation in the yield of albacore from the Oregon-Washington fishery cannot be assigned solely, however, to variation in fishing intensity, because the yield also depends on the fluctuations in availability of albacore in the region.

The number of fish available to a fishery at a particular time is often a complex function of abundance and behavior, both of which may be markedly affected by the environment. Influence of the environment upon albacore off Oregon and Washington has been detectable only through relations of sea temperatures to landings of the commercial fishery (Johnson, 1962) and to catches by Bureau vessels (Alverson, 1961). Water clarity, which varies largely with the concentration of particulate matter, also has been thought to affect albacore availability (Murphy, 1959); to date, however, this hypothesis has not been tested off the Oregon-Washington coast. Powell and Hildebrand (1950) noted a relationship of tuna catches with observed ocean conditions; albacore were

caught in blue, warm water but not in green, cold coastal water. As they noted, however, this effect probably is attributable to temperature rather than to water color. Other environmental variables that have received attention as possible determinants of albacore availability and abundance (or density) include salinity and concentration of forage. No examples of observed relations of these factors to numbers of accessible albacore are available, however, and the relation of temperature to albacore was only grossly defined in previous studies.

The purposes of this paper are to describe the environment that albacore encounter when they first enter the region off the coast of Oregon-Washington, to suggest the physical mechanisms that produce these conditions, and to indicate which of these conditions appear to influence the number of albacore available to the fishery.

DATA SOURCES

Data from which distributions of variables were derived were collected in July 1961-64 on Cruises 51, 55, 60, and 66 of M/V *John N. Cobb*, a cooperative program with the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base, Seattle, Wash. (Owen, 1963, 1967a); in July 1961-62 on Cruises BB-290 and BB-310 of R/V *Brown Bear*, Department of Oceanography, University of Washington, Seattle; and in July 1963-64 on Cruises 6307 and 6407 of R/V *Acona*, Department of Oceanography, Oregon State University, Corvallis, Oreg. Data from which averages of catch per unit of effort for the commercial fishery were computed are from Ayers and Meehan (1963) and from James M. Meehan of the Fish Commission of Oregon (personal communication).

OCEANOGRAPHIC PROCESSES AND DISTRIBUTIONS OF VARIABLES

The study area (fig. 1) is part of the subarctic Pacific Ocean and hence exhibits its principal characteristics: dilution of the surface layers by excess of precipitation over evaporation; and presence of a well-defined, permanent halocline in which year-round temperatures are nearly identical with winter temperatures of the surface layers (fig. 2). The oceanography of the subarctic Pacific was reviewed by Uda (1963), and by Dodimead, Favorite, and Hirano (1963).

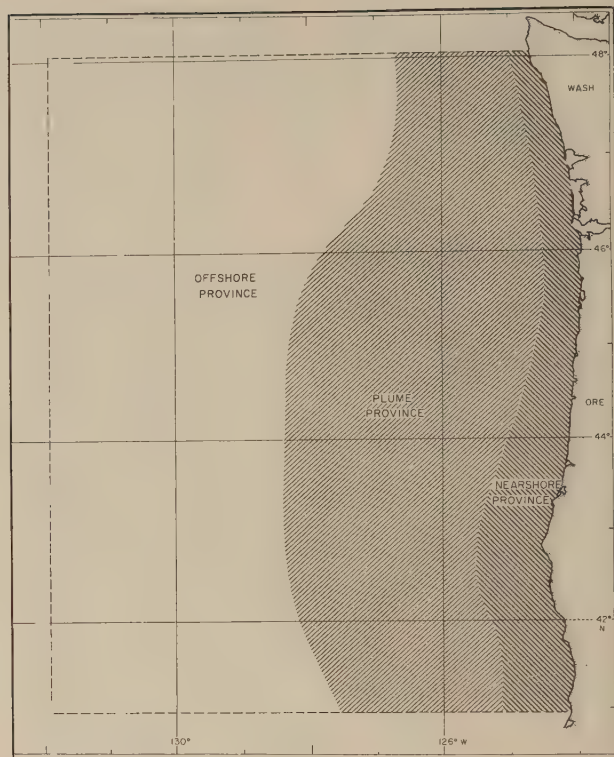


FIGURE 1.—Oceanographic provinces (schematic) off the Oregon-Washington coast in summer. Dashed line represents general limit of study area.

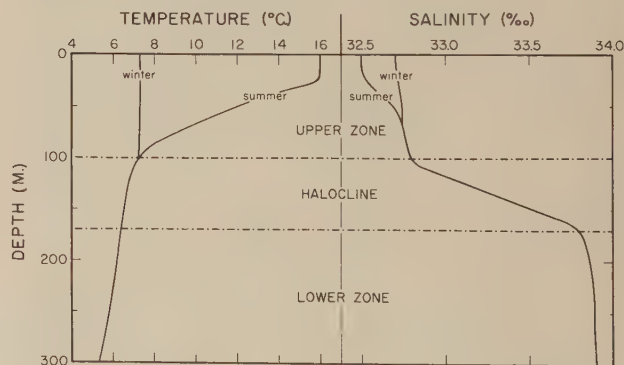


FIGURE 2.—Schematic diagram of vertical temperature and salinity structures in the eastern subarctic Pacific in summer and winter.

Processes that determine the distribution of salt and heat over the subarctic region combine in the study area with effects of nearshore upwelling, river discharge, and bottom topography to produce the distributions of variables reported here. Oceanography in part of the area was reviewed by Budinger, Coachman, and Barnes (1964), and an annotated bibliography on the area influenced by the Columbia River discharge was

prepared by Anderson, Barnes, Budinger, Love, and McManus (1961). An atlas of July oceanographic conditions was prepared as a supplement to the present work by Owen (1967b).

RECURRENT FEATURES OF DISTRIBUTIONS OF VARIABLES

Both in the surface and deep layers, patterns of distribution of physical variables recur from summer to summer over the region off Oregon-Washington. This recurrent nature permits discussion of physical mechanisms that operate in the region.

Upper Zone

Above the main halocline (fig. 2) the area is divisible in summer into three meridionally bounded regions on the basis of physical processes believed to produce the distributions of variables characteristic of each. These regions may be termed nearshore province, plume province, and offshore province (fig. 1).

Nearshore Province.—The first subdivision, nearshore province, lies along the coast in summer as a band of cold, saline water about 50 nautical miles (90 km.) wide, interrupted only by fresher water from coastal sources. It is dominated by the effects of coastal upwelling. Intense horizontal gradients of temperature, salinity, density, and oxygen concentration are encountered from the sea surface to depths exceeding 250 m. (figs. 3, 4, 5, and 6). These gradients result from transformation of offshore vertical gradients, recognized there as the thermocline, halocline, pycnocline, and oxycline, into nearshore horizontal gradients by upwelling.

The offshore summer thermocline (fig. 7) does not coincide with the permanent halocline, but lies above it. Consequently, the corresponding horizontal temperature gradient of the nearshore regime lies farther from the coast than does the horizontal gradient associated with the permanent halocline (compare figs. 7 and 8). Once transported to the near-surface layer by upwelling, water of subsurface origin is warmed by local heat exchange across the sea surface. Because of this local heat gain neither temperature nor temperature gradient permits close assessment of intensity of upwelling, although both serve to indicate the offshore extent of upwelling influence.

The nearshore distribution of salinity is relatively uninfluenced by processes other than diffusion and upwelling in the nearshore province,

except where dilution occurs near coastal sources of fresh water. The water of the offshore halocline is displaced upward within upwelling areas and usually reaches the surface layers. The inshore occurrence near the sea surface of water of the same salinity (33.8‰) as that at the bottom of the offshore halocline (fig. 8) indicates upward transport of water from depths below the permanent halocline. Diffusion and transport across surfaces of constant salinity near shore apparently are important; the near-surface horizontal gradient of salinity in this province is about three orders of magnitude less than the corresponding vertical gradient in the halocline offshore.

Distribution of mass in the nearshore province follows the pattern characteristic of coastal upwelling in general: large horizontal gradients of density are normal to the coastline in the upper layer (fig. 5), and vertical gradients of density are weak. Mass transport probably takes place across surfaces of constant density within the near-surface layers, however, because density is decreased locally there by net heat gain from insolation.

Oxygen concentration may exhibit significant local increase in upwelled water due to photosynthetic processes and to rapid exchange with atmospheric oxygen (fig. 6). These local changes are not sufficiently rapid, however, to obscure the effect of upwelling on oxygen concentration; low oxygen values that denote deep offshore origin are consistently present in surface layers of the nearshore province.

Water in the surface layers of the nearshore province is of deep offshore origin. Water of $\sigma_t \geq 26$, corresponding in density to water near the bottom of the offshore halocline (fig. 9), is common in the nearshore surface layers (fig. 5). The density of some of this water must have been decreased, however, by mixing in transit and by local heating; therefore, it must have come from depths in excess of that of the offshore halocline.

Plume Province.—The second subdivision, plume province, is characterized by near-surface water of low salinity, the result of dilution by coastal fresh water. The Oregon-Washington coast represents a variable line source of fresh water. The Columbia River, however, with a mean annual discharge of $7.3 \times 10^3 \text{ m}^3 \text{ sec}^{-1}$ and a maximum discharge (in June) of about $16.0 \times 10^3 \text{ m}^3 \text{ sec}^{-1}$, contributes more than 73 percent of the average

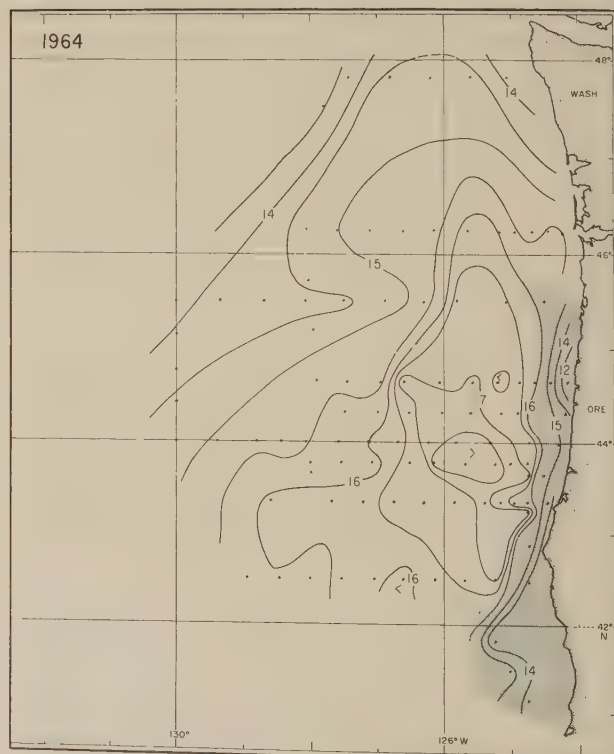
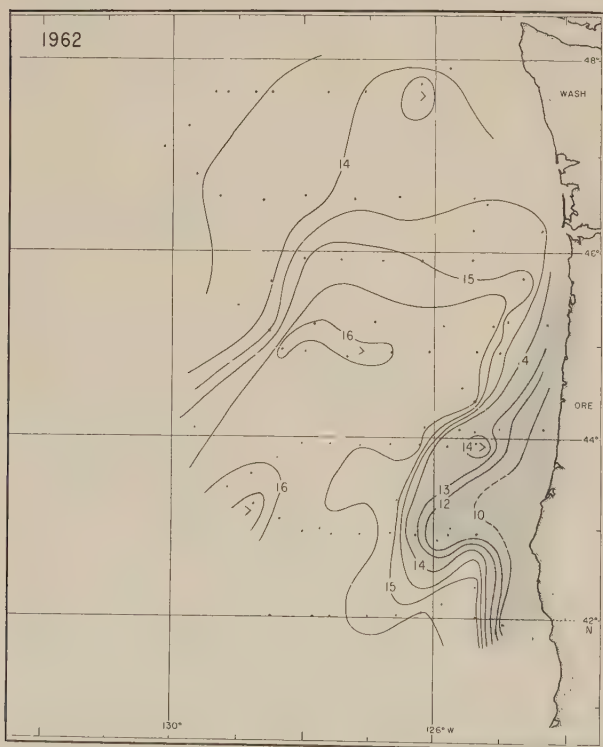
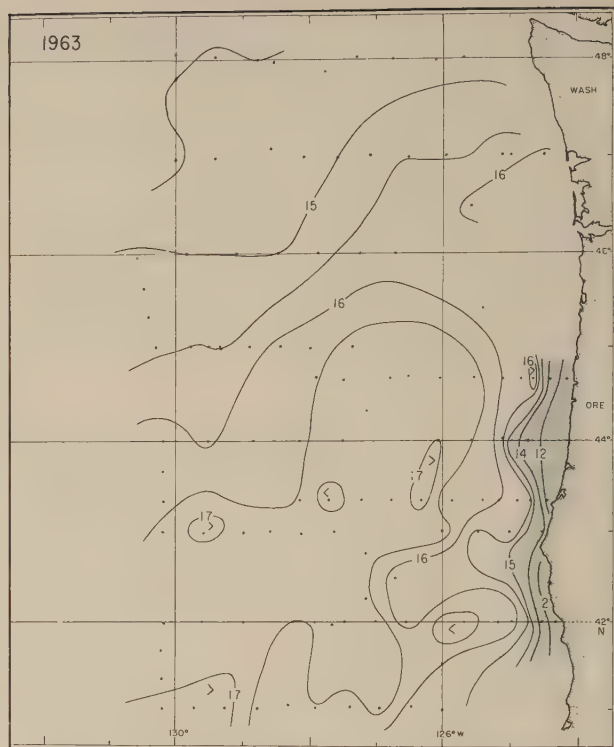
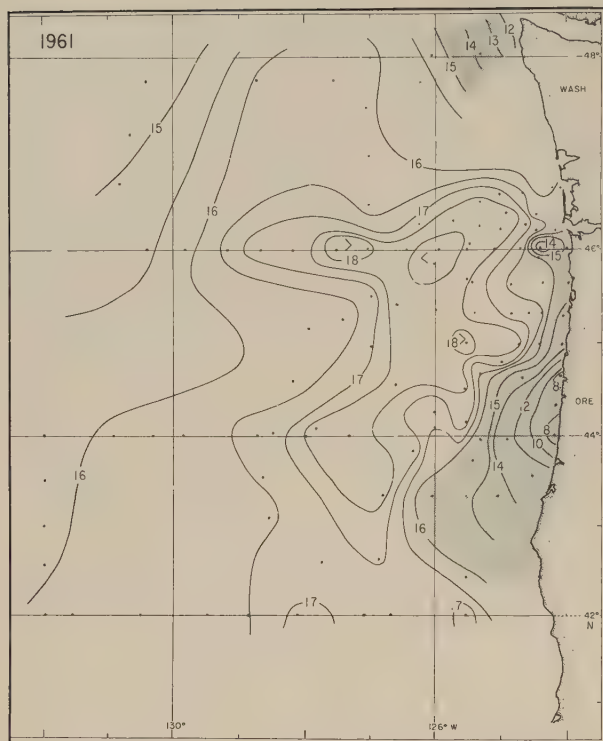


FIGURE 3.—July distribution of temperature at the sea surface, 1961–64. Contour interval is 0.5°C . except where shaded.

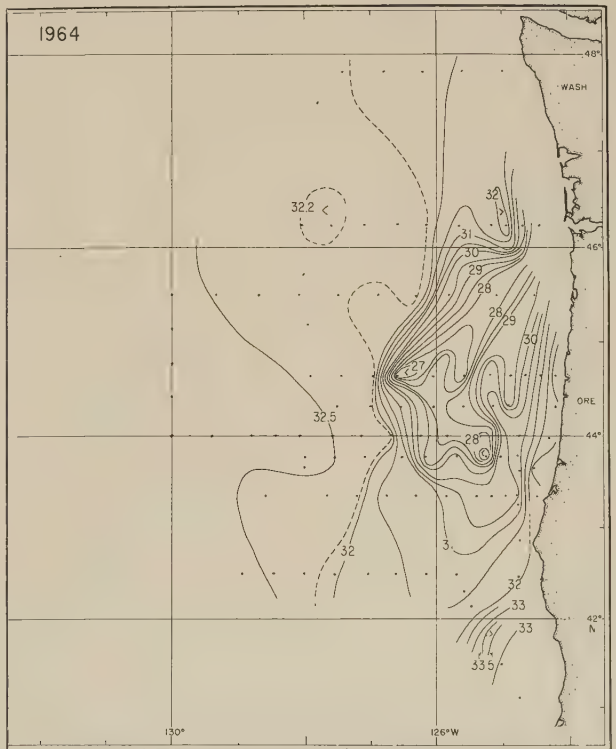
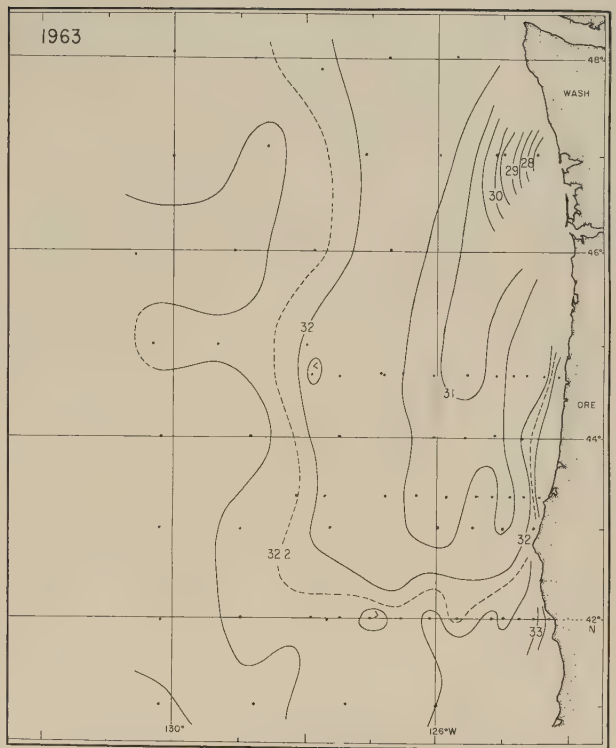
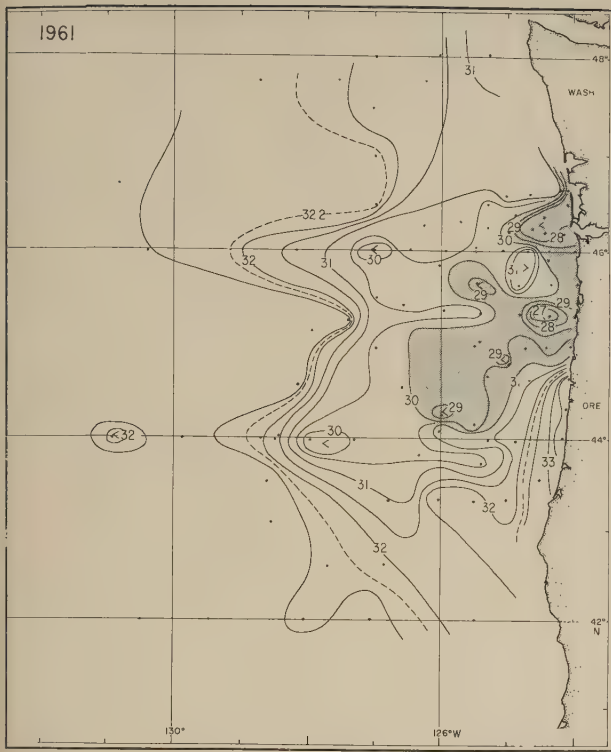


FIGURE 4.—July distribution of salinity at the sea surface, 1961–64. Contour interval is 0.5‰ except where shaded.

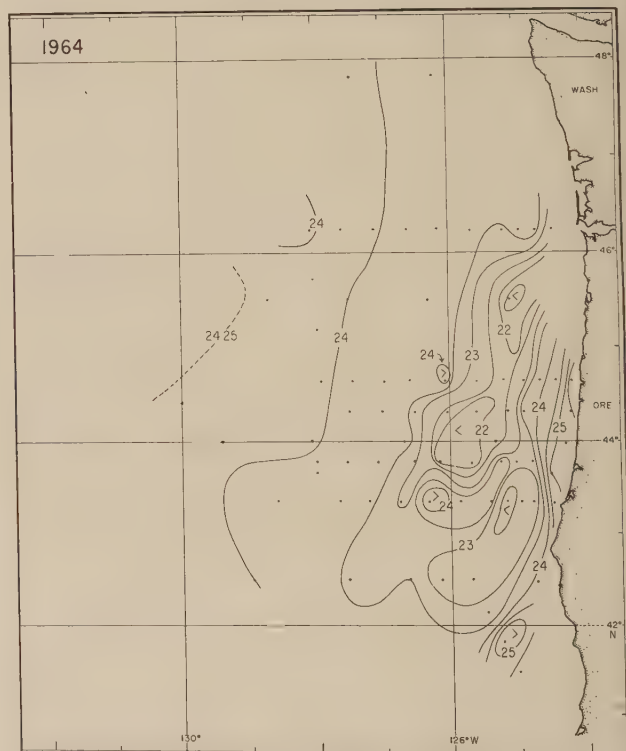
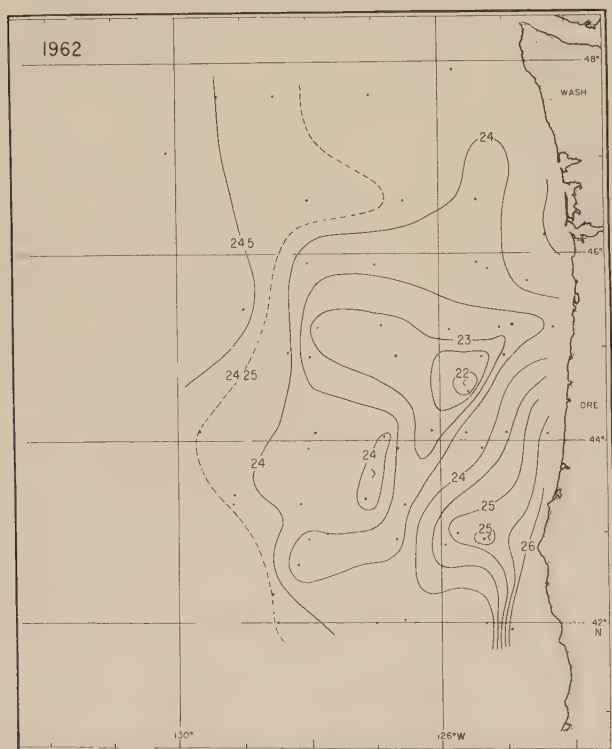
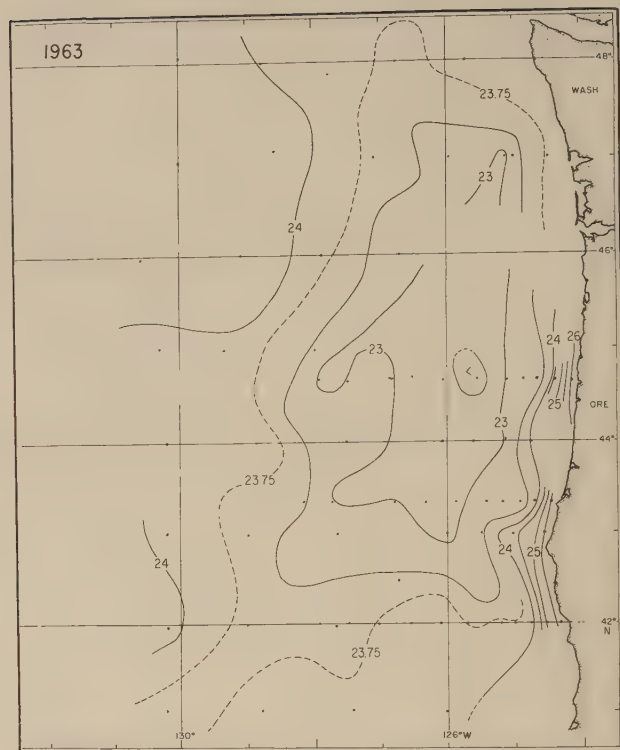
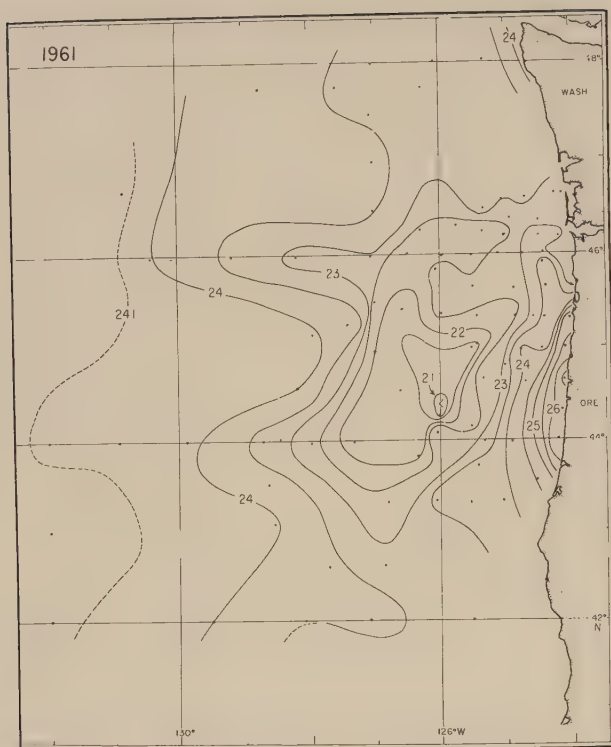


FIGURE 5.—July distribution of density at 10 m. depth, 1961–64. Contour interval is $0.5\sigma_t$ unit.

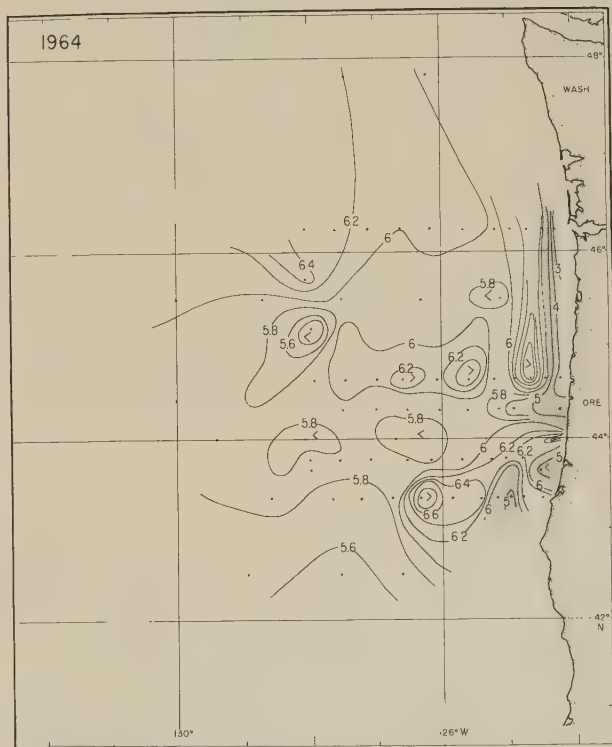
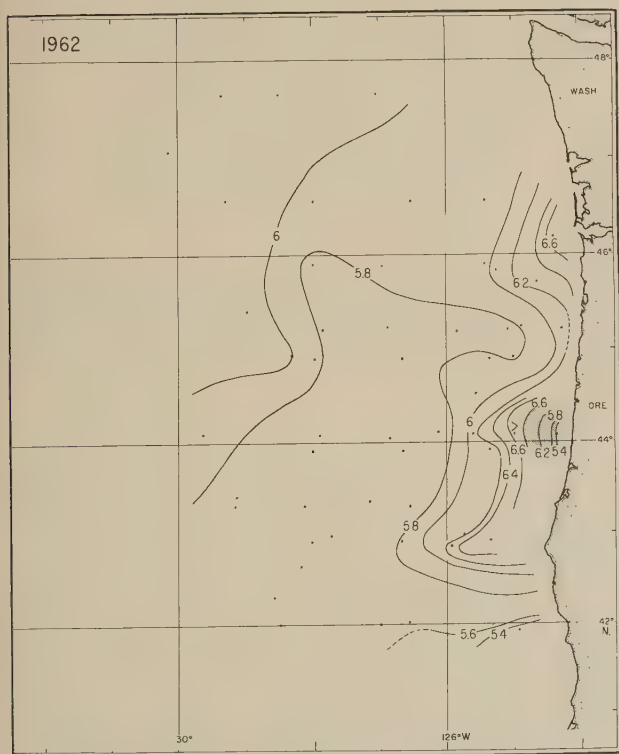
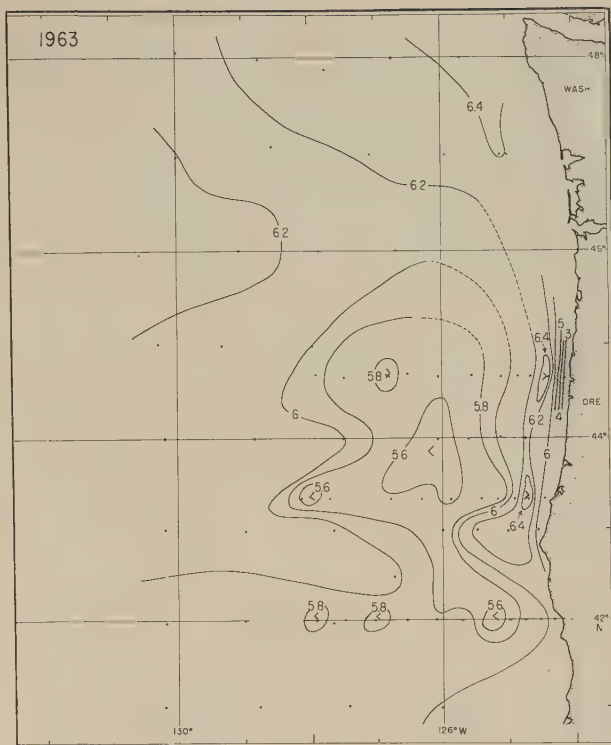
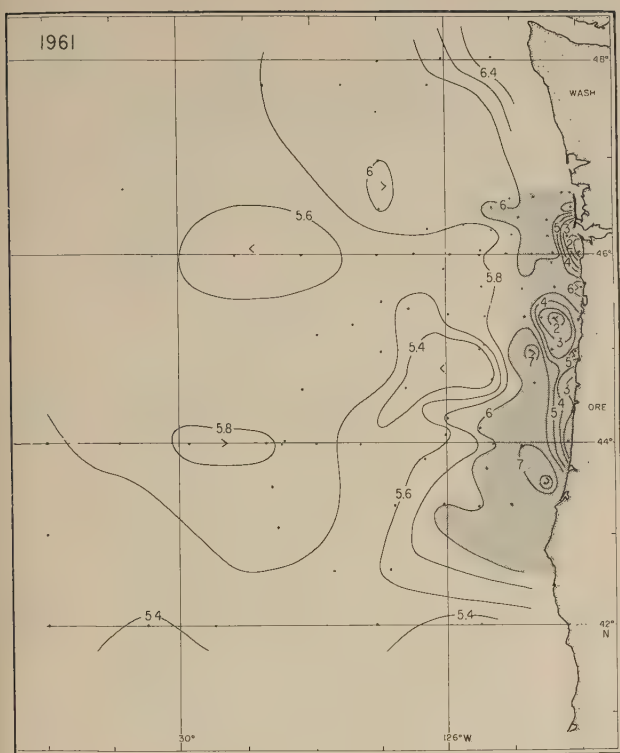


FIGURE 6.—July distribution of oxygen concentration at 10 m. depth, 1961–64. Contour interval is 0.2 ml./l. except where shaded.

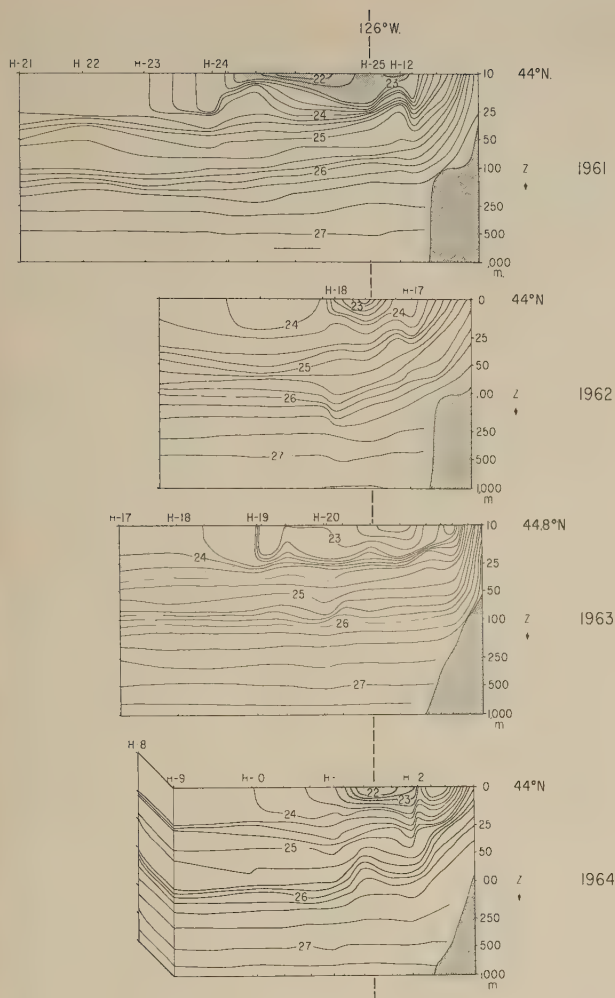


FIGURE 9.—Vertical profiles of July density along lat. 44° N. (approximately). Longitudinal relations between profiles are preserved. Sea floor is stippled. Contour interval is 0.25 σ_t unit except where shaded. Depth scale is logarithmic.

entrainment and diffusion produce lateral and vertical flux of salt into the plume so that the moving parcel loses its dilute character with time and distance from its source until it is indistinguishable from water of offshore origin.

In the present treatment, the 32.2‰ isohaline is the criterion of the plume limit. This value was chosen because 32.2‰ conservatively specifies the largest value of salinity in the salinity gradient at the interface between the plume and surrounding water (figs. 4 and 8), beyond which the immediate physical influence of the plume is much diminished. The plume province thus may be defined as the portion of the area over which sur-

face salinity is less than 32.2‰. Geographic limits of the plume, as defined by Budinger et al. (1964) for examining the fresh-water budget, were given by the location of the 32.5‰ isohaline. By this criterion, plume in summer has been detectable south of lat. 42° N. and as far as 300 nautical miles (560 km.) offshore (fig. 4), although the plume province itself does not extend so far.

The secondary halocline between plume and underlying water partly coincides with the summer thermocline (compare figs. 7 and 8 above 50 m. depth). This superposition notably increases the vertical density gradient $\partial\rho/\partial z$ over the extent of the plume province. Stability, related to the density gradient approximately by $\frac{-1}{\rho} \frac{\partial\rho}{\partial z}$ is also high; in July 1964, for example, average plume stability at $14.2 \times 10^{-7} \text{ cm.}^{-1}$ was about 80 percent greater than average stability in the corresponding pycnocline beyond the plume.

Offshore Province.—The third subdivision, which lies seaward of the plume province, is termed the offshore province. Its character is identical with the eastern extreme of the subarctic region termed “Transitional Domain” by Dodimead et al. (1963), in that it is subarctic water with temperatures in excess of 7° C. at the top of the halocline. The offshore province may also be considered to be part of the upstream source of the California Current, since at least some of the water flows southward off the coast of California. The offshore province exhibits the vertical salinity and temperature structure characteristic of the eastern subarctic as a whole (fig. 2)—a deep, permanent halocline through which temperatures are nearly constant, and a separate, overlying summer thermocline. No strong secondary halocline is present, and salinity increases gradually and continuously with increasing depth through the layer between the summer thermocline and permanent halocline (fig. 8).

Lower Zone

Below the main halocline, coastal runoff has no direct physical influence so that only two provinces, nearshore and offshore, are distinguishable.

The nearshore lower zone is defined here as the region where the field of motion and bottom topography produce significant onshore ascent² of

² Ascent is here considered significant if the slope of isopleths monotonically exceeds 10^{-3} over more than two sampling locations. The term “monotonic” refers in this paper to slopes with no maxima or minima, i.e., $\partial^2/\partial z^2 = 0$.

surfaces of constant density. The seaward limit of the nearshore province is not often well defined but appears to lie farther from the coast than its upper-zone analogue (figs. 7, 8, and 9). This displacement is presumed to occur because upward deflection of coastward flow occurs farther offshore with increasing depth in response to proximity of the sloping sea floor.

Coastal upwelling in the area is largely seasonal and is caused principally by response of surface waters to the spring shift in prevailing wind direction from southwest to northwest (Lane, 1962). Because characteristics of the water in the lower-zone nearshore province are affected by this seasonal process, this province stands in contrast to that of the offshore, where seasonal changes are difficult to distinguish from nonseasonal changes (Tully, Dodimead, and Tabata, 1960).

Depth to which upwelling affects distribution of heat, salt, mass, and oxygen concentration is presumed usually to be less than about 200 m. (Sverdrup, 1938; Doe, 1955). Portions of many of the vertical sections that lie within the nearshore province, however, exhibit significant onshore ascension of isopleths of these variables at depths in excess of 250 m. (figs. 7, 8, 9, and 10).

Located beyond direct influence of bottom topography and seasonal processes, the lower-zone offshore province exhibits the horizontal uniformity of property distributions that is typical of the lower-zone subarctic. Small slopes of surfaces of constant salinity, temperature, and density indicate sluggish circulation, except where deep eddies occur. The recurrent nature of some of the closed-curve patterns that suggest eddylike motion has been noted by Budinger et al. (1964). That these patterns are recurrent implies that they do not result from internal-wave distortion of the mass field or from failure of the assumption that measurements were synoptic—possibilities suggested by Defant (1950).

Currents

The study area is largely shoreward of the region where the West-Wind Drift diverges to feed the California Current to the south and the Alaska gyre system to the north (see Dodimead et al., 1963). Previous works that included the study area (Doe, 1955; Barnes and Paquette, 1957) show weak, variable geostrophic currents that are sensitive to the influence of wind and bottom topography.

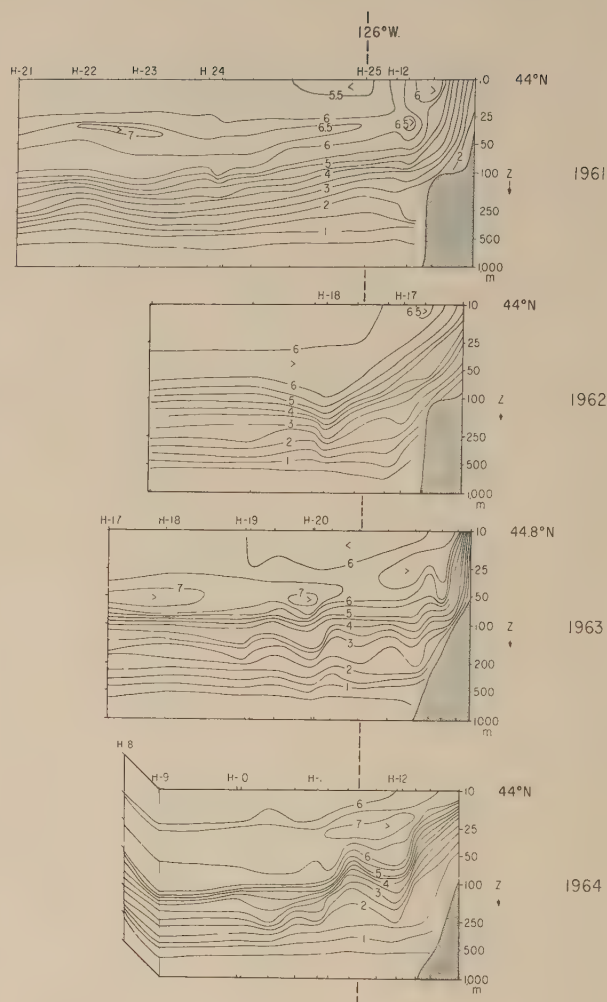


FIGURE 10.—Vertical profiles of July oxygen concentration along lat. 44° N. (approximately). Longitudinal relations between profiles are preserved. Sea floor is stippled. Contour interval is 0.5 ml./l. Depth scale is logarithmic.

The reference level of 500 dbar. (decibars) is used in the present work; this value was selected because data were insufficient below the corresponding geometric depth. Agreement in speed and direction of geostrophic flow referred to the 500 dbar. surface with flow referred to 1,000 dbar., previously accepted as adequate for direction (Dodimead, 1961, and others), is sufficient to warrant use of the 500 dbar. level. Dodimead et al. (1963) presented flow at 500 dbar. with respect to 1,000 dbar. for summers of 1955–59. Their charts, which include the study area, indicate current speeds on the 500-dbar. surface that generally do not exceed 0.8 cm. sec.⁻¹; i.e., they are insignificant. Also, average flow direction referred to 1,000 dbar., and to 500 dbar. by the extension

above, has been shown to agree with independent observations of ship drift over large parts of the North Pacific (Reid, 1961). No single level, however, is strictly appropriate for use as a "level of no net motion" in the subarctic. Drogue measurements in the study area (Budinger et al., 1964) indicated a weak current at 1,000 m. depth, so that slight error from this source is expected in charts of geopotential referred either to surfaces of 500 dbar. or of 1,000 dbar.

Current direction denoted by dynamic topography varies from year to year, particularly in the offshore and plume provinces (fig. 11). Geostrophic speeds, proportional to geopotential gradients, are slow and generally uniform beyond the nearshore province; values of 3 to 8 cm. sec.⁻¹ are typical.

Redistribution of mass due to nearshore upwelling results in a dynamic topography that consistently suggests intensified southerly flow (30–50 cm. sec.⁻¹) near the coast, and an eddy or loop with even greater velocities at about lat. 43° N. It is unlikely, however, that geopotential gradients reflect current velocities in nearshore areas as accurately as in the offshore and plume provinces. Time lags in the response of distribution of mass to changes in wind-driven transport probably negate the assumption of a steady state in the nearshore provinces.

The wind-induced component of flow, the Ekman transport, is superimposed on geostrophic flow in the upper layer of the sea. Ekman transport by blocks of 1° latitude, averaged zonally from longs. 130.5° W. to 124.5° W. in June and July, was calculated from the source and by the method given later in this paper. These averages demonstrate that wind-induced flow is generally to the west or southwest and that the flow—in particular its zonal component—intensifies with decreasing latitude (fig. 12). No such marked tendencies are apparent from analogous meridional averages, except that of direction.

Average current speeds computed from Ekman transport, presumed to extend to 30 m. depth, generally are lower, often by a factor of 10, than geostrophic speeds. The effect of Ekman transport on distribution of variables is probably very important, however, where Ekman transport is not parallel to geostrophic transport—in the nearshore province, parts of the offshore province, and near the plume boundaries.

Tongue Structures

Recurved, tonguelike isopleths are apparent in distributions of temperature, salinity, density, and oxygen concentration over the upper-zone waters. Along any approach to the coast from the offshore province, one thus encounters a maximum in temperature (fig. 3), minimums in salinity and density (figs. 4 and 5), and both a minimum and a maximum in oxygen concentration (fig. 6). These large-scale extremes are mainly confined to the surface layers but occur occasionally at greater depths. Each large-scale extreme, except the oxygen maximum, occurs within the area here defined as the plume province.

The salinity minimum is due simply to the presence of the low-salinity plume. In the absence of runoff, salinity at the sea surface would presumably decrease monotonically from about 33.5‰ in the upwelling areas to about 32.5‰ with increasing distance offshore.

The tonguelike ridge of higher temperatures is ascribable to two effects of the plume itself. Because the secondary halocline at the plume-sea water interface partly coincides with the thermocline, stability is augmented in this interface layer; consequently, downward heat flux through the thermocline is less than that across the unaugmented thermocline of the offshore province. Retention above the thermocline of heat gained in surface layers thus tends to be greater in the plume province than beyond. Second, this greater stability in the plume may be considered to dictate a preferred site for development of the summer thermocline at depths generally less than 20 m.³ Wind-mixing in the offshore province, in the absence of the effect of the plume on stability, is effective to greater depths. The offshore thermocline accordingly develops at greater depths in the manner described by Tully and Giovando (1963). By this difference in mixed-layer depth (depth to the top of the summer thermocline), heat gained in the surface layer is constrained to a smaller volume in the plume than offshore, and hence the plume province has higher summer temperatures. The shoreward decrease of temperature in the nearshore province results simply from upwelling of cold water.

A measure of the extent to which the plume

³ With the partial exception of July 1963, the offshore limit of the plume province is in fact approximated by the 20-m. isopleth of thermal mixed layer depth (fig. 13).

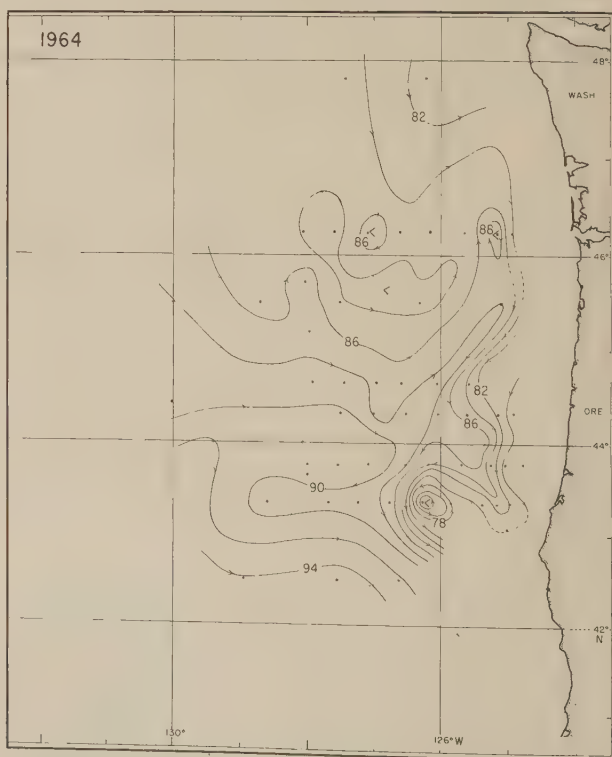
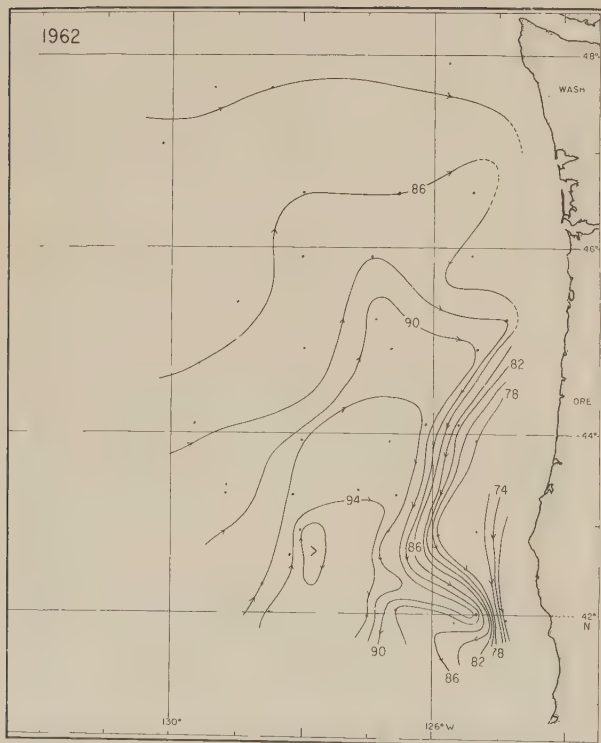
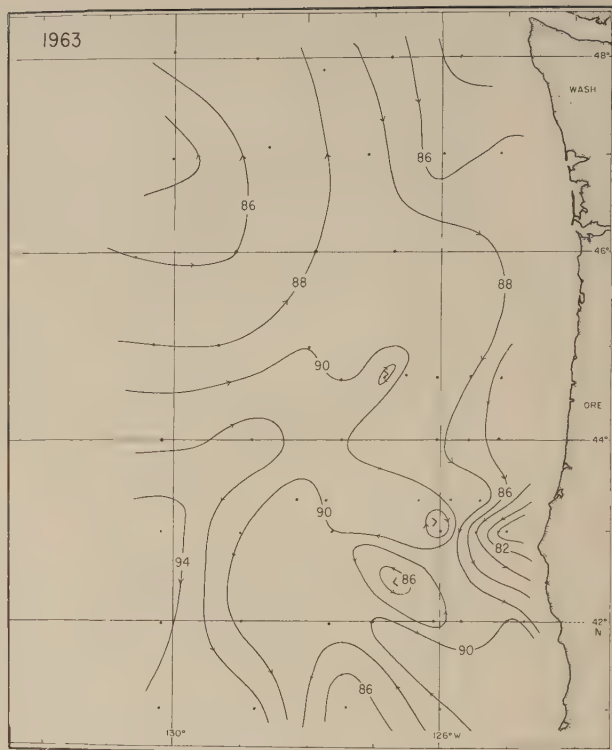
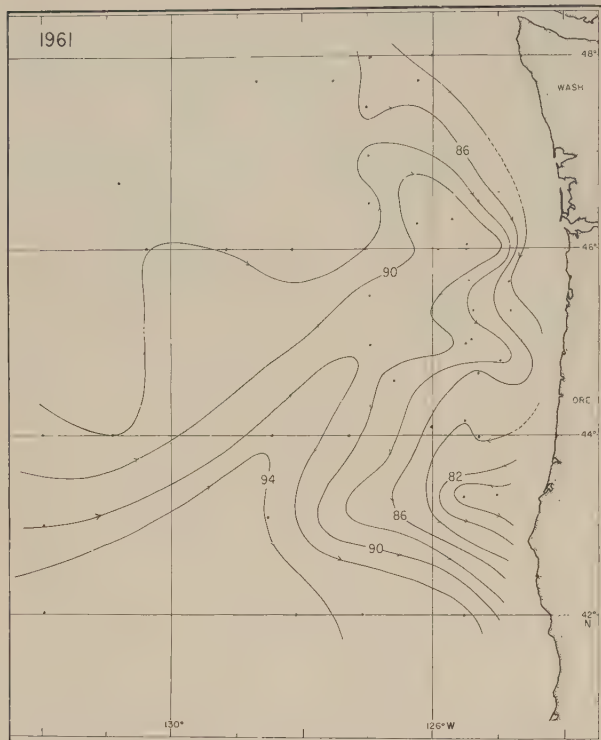


FIGURE 11.—Geopotential topography of the July sea surface relative to 500 dbar., 1961-64. Contour interval is 2 dynamic cm.

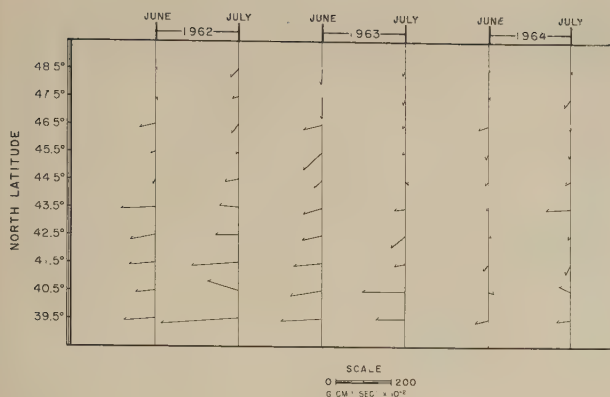


FIGURE 12.—Wind-driven (Ekman) transport vectors by 1° increments of latitude, averaged between longs. 124° W. and 130° W. Length of vectors gives transport in $\text{g. cm.}^{-1} \text{sec.}^{-1}$ according to the scale below figure.

influences heat constraint, and therefore temperature distribution, is provided by figure 14. As implied by figure 2, the permanent halocline is the lower limit of winter mixing; consequently temperature near the top of the permanent halocline is nearly identical to that of the mixed layer in the previous winter (Dodimead et al., 1963). Hence the July difference between temperature at the sea surface and the temperature where salinity equals 33‰ , located within the halocline, is a measure of mixed-layer temperature change, $\Delta\theta$, from the previous winter. The area of greater temperature change substantially corresponds to the plume province as defined by surface salinity distributions (fig. 4).

The summer tongue of lower density in the plume province (fig. 5) is produced by the coincidence of tongues of low salinity and high temperature described above.

Distribution of oxygen concentration in the near-surface layers is more complicated than that of the preceding variables. Shoreward of the minimum (5.4–6.5 ml./l.) in the plume province are a maximum (6.6–8.0 ml./l.) in the seaward portion of the nearshore province and a minimum (2.0–5.0 ml./l.) nearest the coast. These extremes combine to produce the trough-and-ridge oxygen distribution that was characteristic of the area in each summer in 1961–64, except the last (fig. 6).

The oxygen minimum in the plume is the result of the larger influence of reduced oxygen solubility at higher temperatures over the opposite influence of higher oxygen solubility at reduced salinities. Since the degree to which waters of the

surface layer are saturated with oxygen is the same in the offshore as in the plume province (about 104 percent), this variation is not attributable to differences in biological processes.

In the horizontal distribution of oxygen, the presence of both the minimum and maximum concentrations in the surface layer of the nearshore province is the product of one or both of two effects of upwelling. Upwelling transports nutrient-rich water that is undersaturated with oxygen into the photic zone, where algal photosynthesis increases the oxygen concentration sufficiently to produce supersaturation. If the transfer of oxygen from the air to the sea proceeds faster than the transfer of heat, supersaturation can result independently from this purely physical process. The oxygen minimum along the coastal portion of the nearshore province may thus represent that part of the upwelling system where the residence time of low-oxygen water in the surface layer has been too short to exhibit effects of local oxygen gain by photosynthesis and atmospheric exchange. Conversely, the maximum in the outer part of the nearshore province represents the area where one or both processes have been operating for sufficient time to effect supersaturation. Large standing stocks of phytoplankton, indicated by higher chlorophyll concentrations (Owen, 1967b) and larger rates of carbon assimilation nearshore (Anderson, 1963), support the hypothesis of greater oxygen production by photosynthesis in the fertile nearshore province than beyond. That local processes of oxygen gain are effective in this province is evident from the decreased slopes of near-surface oxygen isopleths (fig. 10) relative to isohaline slopes (fig. 8). In the absence of local oxygen gain, these slopes would be identical.

The nearshore maximum in the horizontal distribution of oxygen may also be ascribed to a more direct effect of upwelling. Seaward of the nearshore province, a maximum value (5–7 ml./l.) in the vertical distribution of oxygen concentration occurs in summer at depths of 30 to 70 m. (fig. 10). This maximum is not confined to the present area, but is present over large parts of the North Pacific, where it has been ascribed to summer loss of oxygen above the layer in which the maximum occurs (Reid, 1962; Pytkowicz, 1964). Summer upwelling in the nearshore province would displace the layer of this oxygen maximum upward to form the horizontal maximum in the

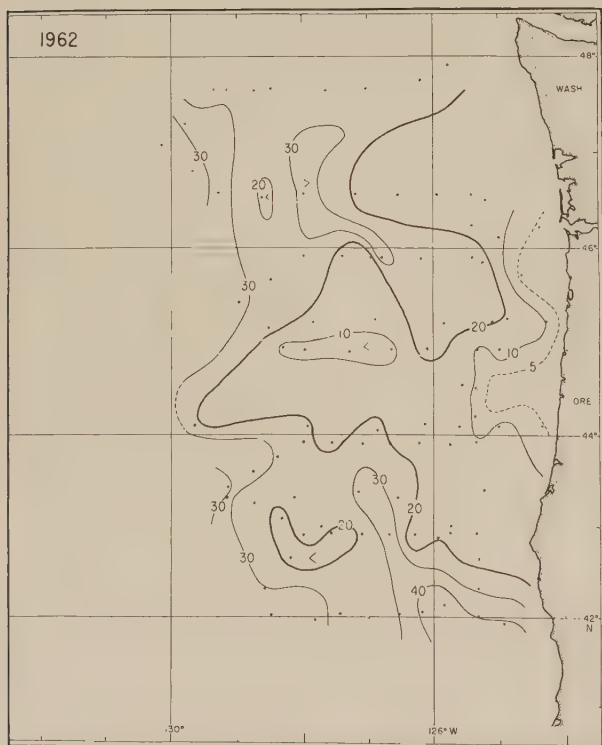
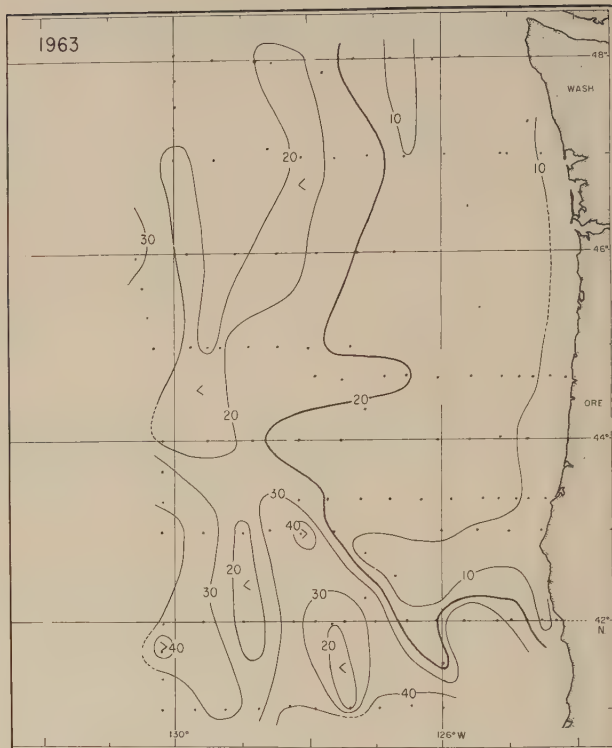
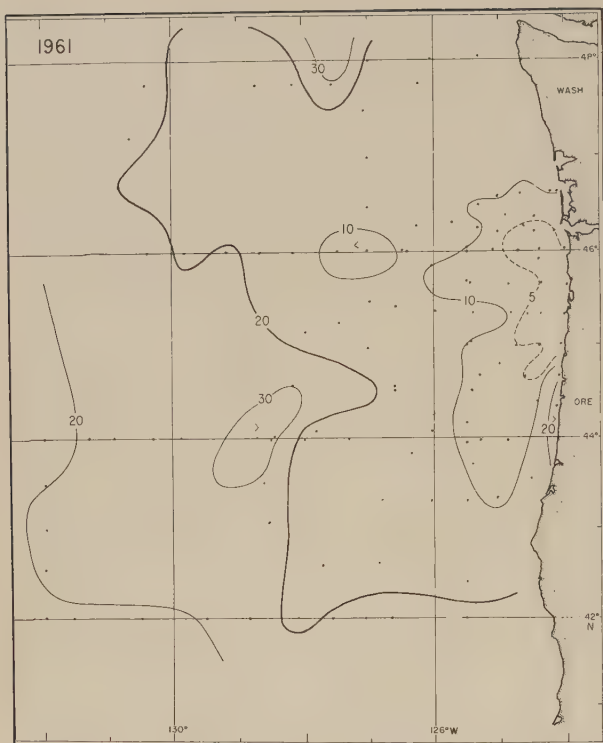


FIGURE 13.—Depth of the upper mixed layer in July 1961–64. Contour interval is 10 m.



FIGURE 14.—Difference between surface-layer temperature and temperature at the depth where salinity equals 33‰, 1961–64. Contour interval is 0.5° C.

near-surface layer (fig. 6). Stefánsson and Richards (1964, p. 374), on the other hand, have suggested that offshore movement and subsequent sinking (along isentropic surfaces) of upwelled water which has gained oxygen from photosynthesis would "largely contribute to the formation of the (offshore vertical) maximum." If so, then the near-surface horizontal maximum would presumably result. It seems unlikely, however, that this process alone could generate the vertical maximum that occurs widely over the North Pacific; definitive measurements—e.g., apparent phosphate uptake (APU) in the layer of the offshore oxygen maximum—are not yet available to indicate whether the vertical oxygen maximum of the plume and offshore provinces is derived from the nearshore, near-surface horizontal maximum, or, conversely, whether it produces the nearshore maximum by upward displacement.

Oxygen distribution in the near-surface layer apparently was atypical in the summer of 1964 (fig. 6). The basic pattern described above was altered in the plume by the presence of well-developed pockets of high concentrations of oxygen. Production of some pockets by phytoplankton photosynthesis is indicated from their high degree of supersaturation (106–110 percent) and from generally large concentrations of chlorophyll *a* in the plume and offshore province in 1964. High-oxygen pockets were associated with low temperatures (13–14.5° C. at 10 m.). Heterogeneity of their mode of generation is indicated, however, by the large corresponding range of salinity (30.5–32‰ at 10 m.), and one pocket, centered at lat. 43.3° N. and long. 126.2° W., clearly was produced as part of a dome formed by the motion of a cyclonic eddy (fig. 11).

Tonguelike patterns occur occasionally at greater depths (100 m. or more) but not with sufficient frequency to be considered recurrent or characteristic. It is difficult to see how these tongues could arise from the same mechanisms that produce near-surface tongues. Because of the nearly uniform temperature-salinity relation beneath the near-surface layer, the tongues at the greater depths appear to be produced by the distribution of mass associated with geostrophic flow.

ANNUAL VARIATIONS

Differences from year to year in extent and character of provinces are generated by changes

in the dominant processes. The basic patterns discussed in the previous section are not obscured, however, but are altered only in degree. Effects of these differences upon heating in the surface layers are discernible.

Extent and Character of Provinces

The state of development of the nearshore province is determined principally by the intensity and duration of upwelling, which in turn depends upon the nature of the coastal wind field and upon local bathymetry. Because bathymetry is fixed, between-year differences in the extent of the nearshore province should be assignable to differences between years in the June and July wind fields. A means of assessing the effect of wind field on upwelling is provided by estimation of average zonal components of Ekman transport across the near-coast meridian 124.5° W. Wind data for the study area in June and July 1962–64 were obtained from monthly summaries of marine weather observations for the Pacific Ocean prepared by the Tuna Resources Laboratory, Bureau of Commercial Fisheries, La Jolla, Calif., in the form of average zonal and meridional components of wind velocity by 1° squares. Average wind stress, $\bar{\tau}$ (g. cm.⁻¹ sec.⁻²), was computed from average wind velocity, $\bar{U}$ (assumed to have been measured at 10 m. above sea surface), by the basic equation

$$\bar{\tau} = \rho C_D U^2$$

where air density, ρ , is taken to be constant at 1.2×10^{-3} g. cm.⁻³ and $C_D = (1 + 0.07U) \times 10^{-3}$ (Deacon and Webb, 1962, p. 61). The computing equation, with constants adjusted for the use of U in knots, is

$$\bar{\tau} = 0.318 \bar{U}^2 (1 + 0.036 \bar{U}) \times 10^{-2} \quad (1)$$

Because instantaneous values of wind velocity were not available from the summary described above, equation (1) was entered with averaged values of wind speed ($\bar{U}$). Because $(\bar{U})^2 < \bar{U}^2$, values of $\bar{\tau}$ used here underestimate the true averages of wind stress.

Ekman transport, which is assumed not to extend beyond the bottom of the pycnocline produced by the thermocline and plume halocline, is given by integration of equations of motion with appropriate boundary conditions:

$$M_x = \tau_y / f$$

$$M_y = \tau_x / f$$

where f , the Coriolis parameter, is evaluated for present purposes at lat. 45° N. The zonal component was computed for each degree of latitude from 39.5° N. to 48.5° N. along long. 124.5° W., and then averaged to give mean zonal transport in $\text{g. cm.}^{-1} \text{ sec.}^{-1}$ for June and July 1962–64. The results indicated that the intensity of upwelling was highest in June and July of 1962, when the offshore transport across 124.5° W. was largest, and lowest in June and July of 1964, when offshore transport was least (table 1). Wind data are not available for June and July of 1961.

TABLE 1.—Average zonal component of Ekman transport, $M_z (\text{g. cm.}^{-1} \text{ sec.}^{-1} \times 10^{-3})$, westward across long. 124.5° W. from lat. 39.5° N. to 48.5° N., for June and July 1962–64

Year	June	July	Average
1962.....	6.77	8.75	7.76
1963.....	3.67	5.89	4.78
1964.....	3.34	0.72	2.03
Average.....	4.59	5.12	4.86

Correspondingly, oceanographic evidence indicates greater upwelling in 1962 than in 1963 or 1964. Local heating of upwelled water, as pointed out previously, precludes use of near-surface temperature and density for assessment of upwelling. Salinity, however, is little changed by processes other than diffusion and upwelling, and thus provides the best available estimator of upwelling effects. The extent of the nearshore province and, therefore, July development of upwelling may be compared between years by noting the distance from the coast at which the 32.5‰ isohaline is first encountered at the sea surface. The mean distance of this isohaline from the coast was about 50 nautical miles (90 km.) in 1962, but less than 20 nautical miles (35 km.) in 1961, 1963, and 1964. These distances indicate a significant seaward extension of the nearshore province in 1962. The rather precise nearshore coincidence of the 32.5‰ isohalines in 1961, 1963, and 1964 suggests close similarity of upwelling in these years and further heightens the contrast of 1962 conditions. Similar checks on the near-surface distributions of other less conservative properties (temperature, density, oxygen concentration) confirm qualitatively that upwelling effects were markedly pronounced in July 1962. Secondary effects of differences were not apparent; extremes were observed in the plume in years when intensity

of upwelling in the nearshore province was similar.

Closer correspondence of June transport than of July transport to the July distributions of properties suggests an appreciable time lag in the response of the nearshore province to changes in wind field. Prediction of upwelling conditions by computations from coastal wind field of the previous month may thus be possible.

The extent and character of the plume province have exhibited the greatest variation from year to year. Differences in size and intensity of the plume itself, shown by comparison of values and gradients in near-surface salinity distributions (fig. 4), suggest large year-to-year differences in the balance of processes that determine plume distribution—volume of discharge from land, diffusion, and advection.⁴ For the period 1961–64, summer conditions in 1963 and 1964 displayed maximum contrast. The plume in July 1963 showed the weakest development; though the area was large the salinity was high and the horizontal gradients were exceedingly small. In spite of less than normal June discharge of fresh water into the province, the depth of the secondary halocline in the plume was not notably less in 1963 than in other years (fig. 8). The small horizontal gradients and large values of salinity in the upper layers of the plume thus show that lateral diffusion and zonal advection were relatively more effective than meridional advection in distributing plume water. Indeed, the smaller zonal gradients of dynamic height of July 1963 (fig. 11) indicate diminished southward transport by the geostrophic component of motion, whereas wind-velocity fields in June and July 1963 indicate large offshore displacements by the Ekman component of motion (fig. 12), particularly to the south of lat. 44° N.

The July 1964 plume, at the other extreme, was highly constrained and was characterized by low salinities ($< 27\text{‰}$ at one offshore station) and by large horizontal gradients of salinity. The meridional constraint of the 1964 plume, together with the observation that the discharge in June 1964 from the Columbia River was largest of the years considered (table 2, last column), indicates dominance of meridional advection over zonal advection

⁴ The effects of time-dependent hydraulic mixing near fresh-water sources, which presumably would determine the characteristics of water in the plume province, are here considered to have been "averaged out" in the time required for water to transit the nearshore province and enter the plume province.

and diffusion in plume dispersion. In contrast to flow conditions in 1963, southward transport by the geostrophic component of motion in July 1964 is indicated to be larger (fig. 11) and to predominate over transport by the much diminished Ekman component of June and July 1964 (fig. 12).

The plumes of 1962 and 1963 would be expected to be similar on the basis of the similarity of June-July wind-induced transports (fig. 12) and of June discharge rates from the Columbia River. They differed markedly, however, in salinity. Although the 1962 plume was nearly as broad as that of 1963, it displayed larger gradients and smaller values of salinity; these differences imply reduced importance of diffusion processes during 1962. Because wind effects were about equal in the 2 years, differences in the geostrophic component of flow must have caused this difference in the relative importance of diffusion, and (together with variation in river discharge volume) the differences in salinity characteristics of the plume. Comparison of dynamic height patterns of the 2 years (fig. 11) reveals two significant differences in the nature of geostrophic flow: greater current speeds and a pronounced northward component in the outer plume province and offshore province in 1962. The apparent reduction of diffusion effects relative to advective effects in 1962 was accomplished by faster geostrophic transport of the plume. Further, the breadth of the 1962 plume and the lateral disposition of pockets of less saline water could have been the consequence of transport of the plume from southwest to northeast, indicated by geostrophic flow in the offshore part of the study area.

Geostrophic flow in 1961 was similar to that of 1962 in current speeds and in the presence of the offshore northward component; probably the plumes of the two years were produced by the same balance of forces. The principal difference

between the two plumes was in salinity—the 1961 plume was less saline than that of 1962. This difference appears to have resulted from high runoff in 1961: average discharge rate of the Columbia River for June 1961 was about $1.7 \times 10^4 \text{ m}^3 \text{ sec}^{-1}$ or 1.5 times greater than the discharge for June 1962 (estimated from Budinger et al., 1964, fig. 34, p. 51).

Differences between years in near-surface salinity of the offshore province were insignificant.

Heating

The general effect of the fresh-water plume on temperature was described above. Briefly, heat is constrained to a smaller volume in the plume than beyond so that, by July, plume temperatures exceed offshore temperatures. Because the degree of plume development varied widely from summer to summer during 1961–64, one may reasonably expect to see variations among the respective temperature distributions.

Temperature of the mixed layer in July at any location in the study area may be considered to be the net expression of the following factors: temperature at the start of the heating season (about March); heat gain, principally across the sea surface, between March and July; heat loss by advection and diffusion; and depth over which heat changes are distributed (thickness of the mixed layer and thermocline). If it is assumed for present purposes that advective heat change is important only in the nearshore regime (as upwelling), and that the meridional gradient of heat-exchange across the sea surface is constant while the zonal gradient is zero over the study area, then one must only consider variation of initial temperature, lateral and vertical diffusion, and free-mixing depth to explain the mixed-layer temperature patterns of figure 3.

July temperature near the top of the permanent

TABLE 2.—Maximum temperature changes and salinity gradients in the plume province and average discharge rates of the Columbia River, 1961–64

[Ranks are provided to facilitate comparisons]

Year	Mid-plume temperature change from previous winter to July		Average vertical salinity gradient at plume boundary, lat. 44° N. in July		Average horizontal salinity gradient normal to plume boundary in July		Average of the Columbia River discharge rate in June	
	$\Delta\theta$ (°C.)	Rank	$\frac{\partial S}{\partial z}$ (‰ m. ⁻¹)	Rank	$\frac{\partial S}{\partial n}$ (‰ km. ⁻¹)	Rank	$\frac{\partial V}{\partial t}$ (10 ³ m. ³ sec. ⁻¹)	Rank
1961.....	8.5	2	0.6	2	0.041	2	17.0	2
1962.....	7.5	3	.4	3	.022	3	11.9	3
1963.....	7.0	4	.2	4	.006	4	11.7	4
1964.....	9.5	1	1.0	1	.092	1	17.5	1

halocline, as noted above, is a measure of the minimum mixed-layer temperature of the previous winter. By definition, minimum temperature occurs at the beginning of the heating season. Seaward of upwelling influence, distribution of July temperature at 100 m. thus approximates the initial field of temperature. Temperature variation at this depth did not generally exceed 1°C . over the plume and offshore provinces, either spatially or from year to year (Owen, 1967b). Compared with spatial and temporal temperature changes in the near-surface layer, this variation was small enough to permit the assumption that none of the variation of July mixed-layer temperature was due to initial temperature differences.

Two sources of variation remain: thermal diffusion and mixing depth. Both may be expected to be substantially affected by salinity gradients at plume-sea interfaces, so that their effects on temperature distribution may be treated collectively as the "plume effect." It is this influence to which the recurrent ridge of higher temperatures was ascribed in the previous section.

On this basis, the validity of the proposed plume effect can be examined by comparing the pattern of plume disposition with the pattern of near-surface temperature change from the respective winters. Average values of salinity gradients normal to the plume edges were estimated from figure 4 (horizontal gradient estimates) and figure 8 (vertical gradient estimates along lat. 44°N .) and entered with values of maximum within-plume temperature change in table 2. The association of larger temperature change within the plume with large plume-edge gradients is clear from this table as well as from the figures themselves.

To examine the plume effect further, mixed-layer temperature change, $\Delta\theta$, was plotted as a function of surface salinity for each July of the 4 years on the basis that surface salinity inversely represents the degree of "presence" of the plume and hence the magnitude of its interface gradients. Sets of paired data from each hydrographic station for each year were subjected to Spearman's rank-difference correlation test (Tate and Clelland, 1957); testing showed significant inverse relation at levels of $p < 0.001$ for 1961, $p < 0.001$ for 1962, $0.1 < p < 0.2$ for 1963, and $p \ll 0.001$ for 1964. Differences between these levels of significance appear to depend on the degree of plume development and salinity gradients.

Validity of the assumed sea surface heat-exchange field must remain an open question. It is difficult, however, to see how the particular field of heat exchange could arise to produce the closed curves of $\Delta\theta$ in the plume regime in the absence of oceanographic mechanisms discussed previously. The lack of advective heat change in the plume and offshore provinces is certain to be an approximation: ridgelike dynamic topography indicates possible advective transport of warmer offshore waters of more southern origin in 1961 and 1962. That this approximation is sufficiently good for showing the plume effect, however, is indicated by the differential heating in the plume in 1964, in spite of a flow pattern that suggests advective transport of colder water from the northwest. Advective effects thus appear to be masked by local change.

SUMMARY OF OCEANIC PROCESSES AND VARIATIONS OFF OREGON AND WASHINGTON

The region studied off the coast of Oregon and Washington is divisible in summer into three oceanographic provinces above and two provinces below the main halocline. This division is based on discontinuities in the distributions of variables that denote discontinuities in the influence of physical mechanisms, so that the oceanographic processes may be considered similar within and dissimilar between provinces. These processes—upwelling in the nearshore province, modification by land runoff in the plume province, and net dilution of surface layers in the offshore province—produce recurrent distributions of heat, salt, mass and, together with biological processes, oxygen.

Annual variations in the distribution of variables are attributable to changes in wind field, in fresh-water discharge from the land, and in advection. The variations are not sufficiently large, however, to obscure the basic patterns generated by dominant processes.

The balance of processes off Oregon and Washington is atypical in one respect. Whereas advection strongly influences recurrent patterns of near-surface distributions in oceanic regions lacking large fresh-water sources, its role in the study area is limited to disposition of land runoff. The low-salinity plume itself establishes the conditions for differences in local processes that generate the recurrent distribution patterns described here.

RELATION OF PHYSICAL PROCESSES TO THE ALBACORE FISHERY

It is particularly desirable to attempt to correlate the environmental conditions encountered each year by albacore when they first enter the region off Oregon and Washington with the subsequent distribution and numbers of fish available to the fishery. Suggested relations of environmental mechanisms to potential success of the fishery (that rarely extends seaward of the plume province) may then be tested in a preliminary fashion.

It appeared early in the analysis that the Oregon-Washington fishery for albacore might owe its degree of success to effects of the plume rather than despite them—i.e., that the limit of the area which contains commercial quantities of albacore might be locally extended to the north by these effects. Larger catches and catch rates of the *John N. Cobb* at and within the lateral limits of the plume than beyond it support the proposal that numbers of available albacore generally are higher in the plume than beyond (table 3, fig. 15).

TABLE 3.—Summary of albacore trolling in July by M/V "John N. Cobb" off the Oregon-Washington coast, 1961–64

[Effort is summed from day of first catch]

Year	Area of catch				Ratio of catch/effort (within/beyond)	
	Within plume ¹		Beyond plume ²			
	Effort	Catch/effort	Effort	Catch/effort	Value	Rank
	<i>Line-hours</i>	<i>No./100 line-hours</i>	<i>Line-hours</i>	<i>No./100 line-hours</i>		
1961-----	802	7.5	647	1.4	5.4	3
1962-----	705	33.3	<10	(³)	(²)	(2)
1963-----	568	24.8	234	0.4	62.0	1
1964-----	202	16.3	183	22.4	0.7	4

¹ Where $S < 32.2^\circ$.

² Where $S > 32.2^\circ$.

³ Catch per unit of effort was not measured because effort was insufficient outside the plume province after the day of first catch within it. On the basis of 316 line-hours expended outside the plume before the day of first catch, however, it can be said that the availability of albacore was far greater within the plume than outside it.

One physical mechanism to which these concentration effects may be related is the greater retention of heat within the surface layer of the plume province. This retention, coupled with wind-induced upwelling in the nearshore provinces, produces the temperature ridge discussed earlier. By extension of previous examples of albacore-temperature relation (e.g. Alverson, 1961; Johnson, 1962) we may assume that, at any instant of the fishery period, albacore will tend to concentrate

in the region where temperature is most nearly optimal and will be absent from regions where surface-layer temperatures are less than 13°C . From smoothed plots of albacore catch frequency as a function of sea surface temperature for the fishery off California (Glenn Flittner, personal communication), 18°C . appears to be the optimal temperature. This temperature is seldom exceeded in the study area in July and is only barely exceeded in August and September. Consequently, after the albacore had moved into the region, we would expect the largest concentrations of fish to develop in the areas with the highest water temperatures or in the plume province rather than in the colder waters of the nearshore or offshore provinces.

Furthermore, in the absence of other environmental effects, relatively more albacore would be expected to be in the plume than outside it in years of greater temperature increase, when the plume is most sharply defined; then catch rates should be higher in the plume province than offshore. This expectation was not upheld, however: comparison of temperature change and plume intensity with average catch rates of fishing by the *John N. Cobb* within the plume province (table 3) and concurrent July–August averages of catch per unit of effort for the commercial fishery in the study area (fig. 16) showed that greater than average numbers of albacore were available in 1962 and 1963, when July temperatures were lower (fig. 3) and temperature changes (table 2, fig. 14) were smaller, than in 1961 and 1964. Furthermore, the ratio of catch rate within the plume to that beyond the plume (table 3) was largest in 1963. These differences in catch rates indicate that albacore concentrated in the plume to a greater degree when the difference in July temperatures in the plume and offshore provinces was least (fig. 3).

These results indicate that at least one variable other than temperature affects the distribution of albacore over the provinces. One factor is variation in catch rate and its relation to abundance of available albacore. If the catch rate for each province adequately represents the number of available albacore, then the ratio of catch rate within the plume to that beyond is free of influence by total abundance of albacore. The agreement of catch rates for exploratory fishing in the plume each year with respective July and August

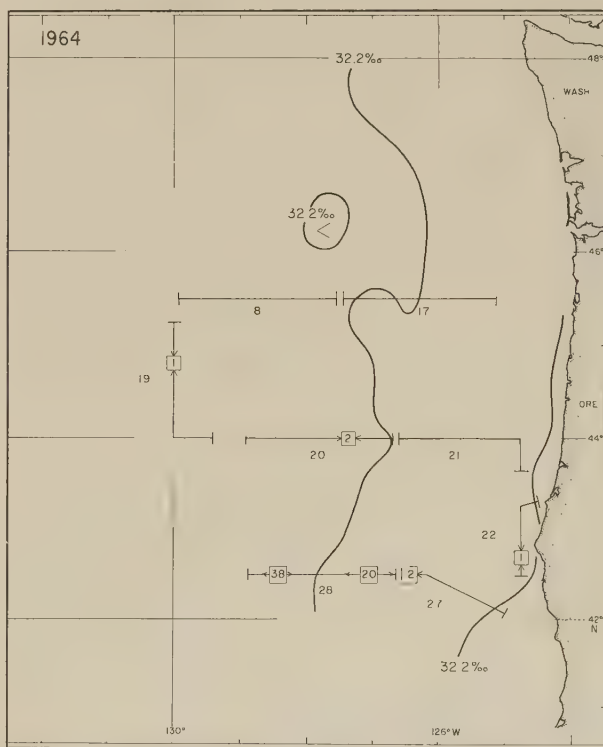
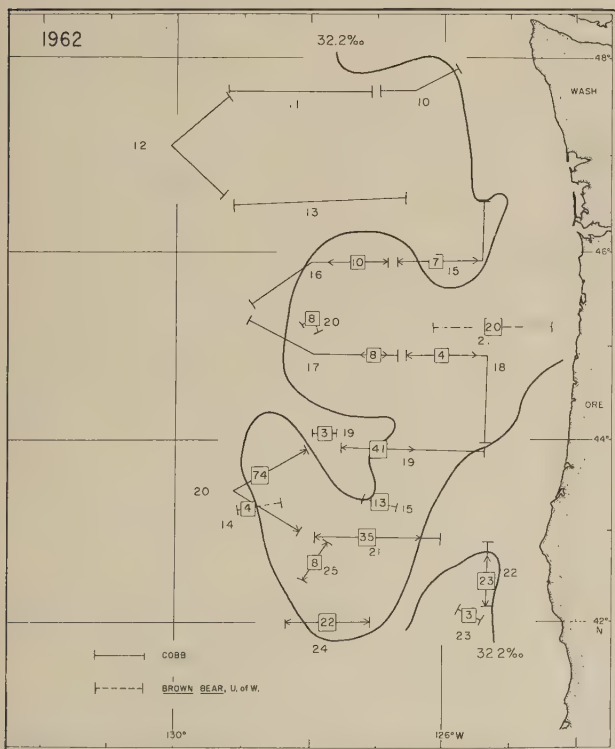
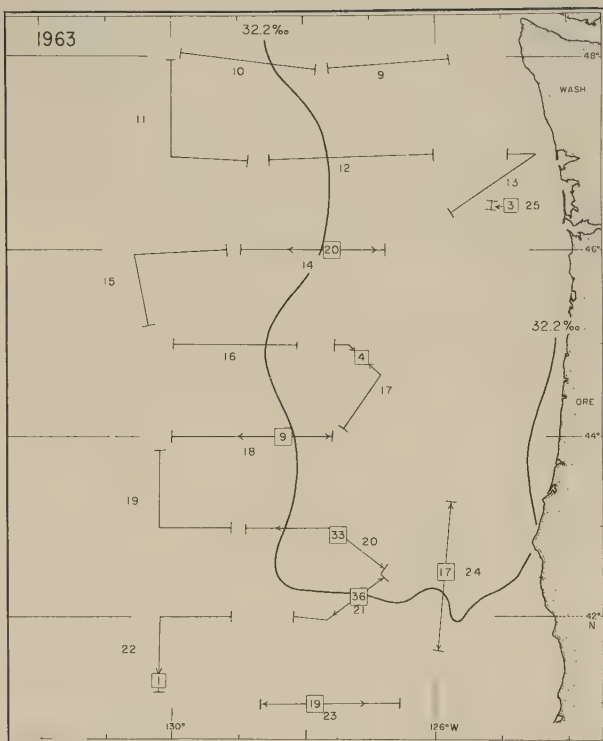
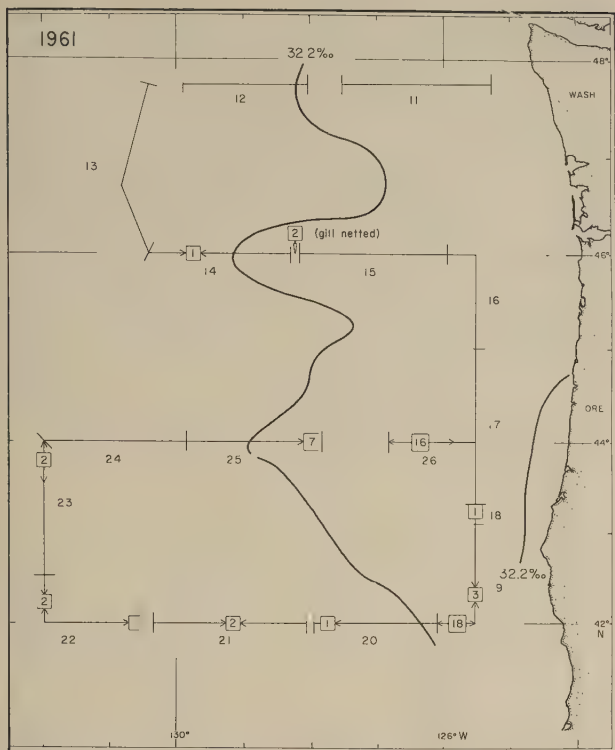


FIGURE 15.—Albacore catches (boxed numerals) by M/V *John N. Cobb* in July 1961–64, with corresponding lateral plume limits (32.2‰ isohaline). July dates are given below or beside track line segments.

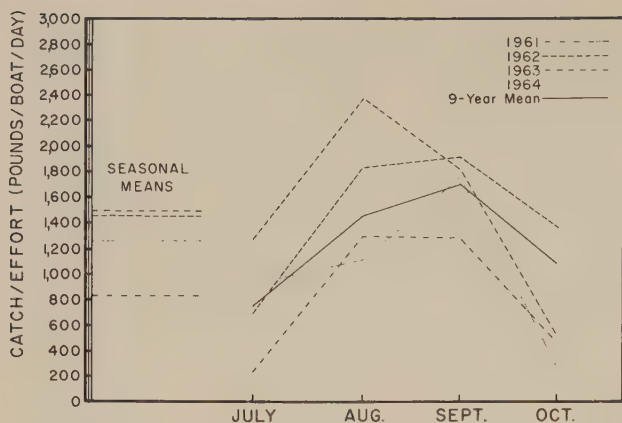


FIGURE 16.—Monthly averages of catch per unit of effort (pounds of albacore per boat-day of fishing) for the area north of lat. 40° N., east of long. 130° W. Data from Ayers and Meehan (1963) and James Meehan (personal communication) for effort exceeding 5 days per 1° square in the month.

catch rates for the commercial fishery in the plume province, although imperfect, indicates that the catch rates for exploratory fishing are adequate for use as ratios in the following discussion.

Still another factor is salinity. Nowhere over their known distribution do migrating albacore encounter a greater range of salinity than in the region off Oregon and Washington. Albacore thus may respond not only to temperature variation, as described above, but also to variation of salinity in the plume—for example through its effect upon balance of osmotic pressure. This balance, the difference between the organism's internal and environmental osmotic pressure (both referred to pure water at 0° C.), was studied by Sakamoto (1962) as a mechanism for determining movements of pelagic fishes and was applied to the Japanese fishery for yellowtail (*Seriola quinqueradiata*, Temminck and Schlegel).

Albacore, like other teleosts, must maintain their internal osmotic pressure at a nearly constant level so that pressure balance is a function only of environmental osmotic pressure. Rewritten from equations of Thompson (1932) and of Lyman and Fleming (1940) in terms of salinity and temperature, the unified expression for osmotic pressure of sea water, π , is (in millibars)

$$\pi(S^{\circ}/_{\infty}, \theta) = (130.067 S^{\circ}/_{\infty} + 5.051) (0.018 \theta + 5.051).$$

Salinity variation clearly dominates variation of

environmental osmotic pressure in the surface layer, and hence the osmotic pressure balance experienced by albacore.

If albacore move so as to maintain a constant balance of osmotic pressure, the response of albacore to more favorable temperatures in the plume would be diminished or even canceled by their negative response to low salinity. Support for a salinity effect is gained by comparing ratios of average catch rates within the plume to rates outside the plume (table 3) with concurrent salinities (fig. 4) and salinity gradients (table 2) in the plume. Salinity and intensity of the plume are inversely ordered with catch-rate ratios (see rank columns in tables 2 and 3).

In summary, I suggest that higher temperatures within the plume, produced by relative constraint of heat, give rise to greater concentration of albacore within the plume province than beyond it once the fish move into the area off Oregon-Washington; plume salinity, to which temperature change is inversely related, qualifies the degree to which temperature difference can be effective (or even negates it during times of extremely low salinity, such as July 1964). Although the now unknown year-to-year differences in total abundance of albacore should be considered in this discussion, the degree to which the proposed mechanisms for differential distribution of albacore are supported by fishery data indicates that variation of albacore distribution over the study area may be as important as variation of total abundance in determining the yield of that fishery.

Results of this study indicate effects of variation of temperature and salinity on albacore distribution. At present experimental information is lacking on physiological and behavioral responses of albacore to such variations. Other factors may affect albacore and may themselves be related to variation of temperature and salinity: the role of forage in the plume province as an attractant to albacore may be worth investigating.

The commercial fishery for albacore off Oregon and Washington has extended infrequently to, and seldom beyond, the offshore limit of the plume province, in part because the range of Oregon-Washington fishing boats is generally short. Consequently, I believe that only a small fraction of the total albacore in the area considered has been exposed to fishing. Results of

this work suggest that the fishery should be extended to the plume limits in most years and farther in years of high plume intensity. Confirmation of the hypothesis presented here will be necessary, as well as useful, by accumulation of more paired observations on plume and albacore distribution. Should the hypothesis be supported, areal differences in catch rate of albacore can be estimated from preseason geostrophic flow, wind field, and Columbia River discharge, because these factors largely determine the physical characteristics of the environment in this region.

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CALANOID COPEPODS FROM THE CENTRAL NORTH PACIFIC OCEAN

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ABSTRACT

A systematic study was made of the calanoid copepods in seven plankton samples collected between lat. 30°00' N. and lat. 42°20' N. along long. 155° W.

Sixty-four species belonging to 17 families are recorded. Measurements, descriptions, and illustrations are given for

most of the species. Two species, *Euchirella unispina* and *Euchaeta wrighti*, are described as new, and the hitherto unknown female of *Centropages elegans* Giesbrecht is described for the first time. *Calocalanus tenuis* Farran is reported for the first time from the Pacific Ocean.

The systematics and distribution of the planktonic copepods of the North Pacific have been widely studied, but such investigations have largely been limited to peripheral waters. Outstanding are the papers by: Esterly (1905, 1906, 1911, 1913, 1924) and Davis (1949) for the eastern Pacific; by Mori (1937), Tanaka (1956a, 1956b, 1957a, 1957b, 1958, 1960, 1961, 1962, 1963, 1964a, 1964b, 1964c), and Vervoort (1946) for the western Pacific; by Brodsky (1950) for the northern North Pacific; and by Grice (1962) for the equatorial Pacific. The copepod fauna of the vast area of the open North Pacific, however, has been relatively little studied, although several early expeditions visited the area and yielded lists of local species (Dana, 1853, 1855; Brady, 1883; Giesbrecht, 1895; Wilson, 1942, 1950).

This paper is devoted to the systematic study of the calanoid copepods in plankton samples from the central North Pacific taken during cruise 29 of the research vessel *Hugh M. Smith* of the Bureau of Commercial Fisheries. Most of the laboratory work for the study was completed at the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, in 1958 and 1959 under a fellowship from the International Cooperation Administration of the United States.

MATERIALS AND METHODS

The materials for this study consisted of seven plankton samples collected between lat.

30° 00' N. and lat. 42° 20' N. along long. 155° W. The samples were taken in oblique hauls with a 1-m. (mouth diameter) net. The front and middle sections of the net were made of 30XXX silk grit gauze (apertures averaging 0.65 mm. in width), and the rear section and bag of 56XXX silk grit gauze (apertures averaging 0.31 mm. in width). The hauls were from a depth of 140 m. and lasted about 30 minutes. The amount of water strained during each haul was measured by a flowmeter in the mouth of the net. The collecting methods for plankton samples adopted by the Biological Laboratory, Honolulu, have been described in detail by King and Demond (1953).

The pertinent data for each plankton sample are given in table 1. Hydrographic data obtained during *Hugh M. Smith* cruise 29 have been published by Graham (1957).

Only small quantities of the original samples were examined. Subsamples were obtained by using the Folsom Plankton Sample Splitter (McEwen, Johnson, and Folsom, 1954). The specimens of each species contained in the aliquot were counted to determine the numerical abundance of the common species. After I had completed the analysis of the subsample, I examined the remainder of the original sample for species not found in the aliquot or to obtain additional specimens, which were often needed to complete the description of a species. Table 2 shows the sizes of the subsamples examined, the list of species and the number of specimens

TABLE 1.—Data on plankton samples collected in the North Pacific Ocean, May 6–13, 1955

[All samples from 140 m. to surface]

Station No.	Position	Date (1955)	Time (local time)	Water filtered
3	30°00' N., 155°00' W.	May 6	0756–0827	1457
5	31°54' N., 154°49' W.	May 7	0742–0818	2390
7	33°54' N., 154°48' W.	May 8	0722–0753	1674
9 ¹	35°52' N., 154°53' W.	May 9	0707–0737	—
13	38°23' N., 154°51' W.	May 11	0715–0748	1851
15	40°08' N., 155°02' W.	May 12	0721–0751	1844
16	42°20' N., 154°57' W.	May 13	0714–0744	1058

¹ The net was torn during the tow.

TABLE 2.—Species and number of specimens in each subsample of plankton—Continued

["X" indicates the species found from collections in the North Pacific Ocean, May 6–13, 1955, in other fractions of original sample]

Species	Station number						
	3	5	7	9	13	15	16
20. <i>Aetideus pacificus</i>							X
21. <i>Euaetideus acutus</i>	4	2	X	1			
22. <i>Euchirella truncata</i>	1	1	X	5	X		
23. <i>E. unispina</i>	3	X	X	6			
24. <i>E. amoena</i>	2	X	X	1			
25. <i>E. rostrata</i>		12	1	18	3	6	
26. <i>Undeuchaeta plumosa</i>		X		7			
27. <i>Euchaeta marina</i>	2	X					
28. <i>E. spinosa</i>	5	6	X	6	X		
29. <i>E. media</i>		X		16	X		
30. <i>E. pubera</i>		1	X				
31. <i>E. wrighti</i> n. sp.	X						
32. <i>Phaenna spinifera</i>	X	X	1				
33. <i>Lophothrix latipes</i>	1	X	X				
34. <i>Scolecithrix danae</i>	16	2	X				
35. <i>S. bradyi</i>	X	X	X	1			
36. <i>Scolecithricella minor</i>							X
37. <i>S. dentata</i>		X				1	X
38. <i>S. ovata</i>		X	X				
39. <i>S. vittata</i>		X					
40. <i>S. auropecten</i>		3	1		1		
41. <i>Metridia lucens</i>							X
42. <i>Centropages bradyi</i>		X		1	38	13	
43. <i>C. elongatus</i>	20	X	X				
44. <i>C. violaceus</i>	X	X	2				
45. <i>C. elegans</i>	24	6	2				
46. <i>Lucicutia flavicornis</i>	8	X	X			X	1
47. <i>Heterorhabdus papilliger</i>		8	2		16	15	7
48. <i>H. abyssalis</i>				4			
49. <i>Heterostylites longicornis</i>		X	X				
50. <i>Haloptilus longicornis</i>	544	44	3				
51. <i>H. fertilis</i>	X	X					
52. <i>H. spiniceps</i>	12	X	X				
53. <i>Augaptilus spinifrons</i>		X					
54. <i>Arietellus aculeatus</i>	4						
55. <i>A. setosus</i>		X	X				
56. <i>Candacia ethiopica</i>	24	2	5	1			
57. <i>C. bipinnata</i>					6	5	X
58. <i>C. varicans</i>	4		X				
59. <i>C. longimana</i>	4	X	X				
60. <i>Paracandacia bispinosa</i>	144	20	1				
61. <i>Pontellopsis regalis</i>	X						
62. <i>Pontellina plumata</i>			X				
63. <i>Acartia danae</i>	4						
64. <i>A. negligens</i>	12	4	X				
Unidentified copepods	26	8	6	21	75	9	14
Number of specimens in subsample	1,190	290	112	190	335	188	457
Subsample size	1/8	1/32	1/16	1/8	1/64	1/128	1/256
Number of copepods per cubic meter	6.5	3.9	1.1		11.6	13.1	110.6
Number of species	33	48	40	21	23	16	14

the northernmost station to 48 at the second southernmost. Except for *Clausocalanus arcuicornis*, none of the species occurred at all the stations. The common species toward the north-

of each found in the aliquot, and the calculated number of copepods per cubic meter of water.

GENERAL REMARKS

The collections contained 64 species of calanoid copepods. Two species, *Euchirella unispina* and *Euchaeta wrighti*, were new. One species, *Calocalanus tenuis* Farran, 1926, had not been previously recorded from the Pacific Ocean. The hitherto unknown female of *Centropages elegans* Giesbrecht, 1895, was discovered and described.

The number of species increased from 14 at

TABLE 2.—Species and number of specimens in each subsample of plankton

["X" indicates the species found from collections in the North Pacific Ocean, May 6–13, 1955, in other fractions of original sample]

Species	Station number						
	3	5	7	9	13	15	16
1. <i>Calanus glacialis</i>		X	1	15	15	9	X
2. <i>C. pacificus</i>					X	8	12
3. <i>C. tenuicornis</i>	40	17	2	2	5	1	
4. <i>C. plumchrus</i>					24	66	376
5. <i>C. cristatus</i>					2	X	
6. <i>Nannocalanus minor</i>	76	85	5	18	1		
7. <i>Neocalanus gracilis</i>	14	30	11	50	5		
8. <i>N. robustior</i>	86	9	6				
9. <i>Eucalanus attenuatus</i>	X	X	X	X	13	10	
10. <i>E. elongatus</i>	10	18	24		34	8	
11. <i>E. bungii</i>		2	13		49	30	30
12. <i>Mecynocera clausii</i>		2	4	1			
13. <i>Paracalanus parvus</i>					1		
14. <i>Calocalanus pavo</i>		X	3				
15. <i>C. tenuis</i>					4		
16. <i>Pseudocalanus minutus</i>							1
17. <i>Clausocalanus arcuicornis</i>	100	7	14	8	38	6	6
18. <i>C. pergens</i>			1		1		
19. <i>Ctenocalanus vanus</i>		1	4	2	4	1	

ern end of the area were *Calanus glacialis*, *C. pacificus*, *C. plumchrus*, *Eucalanus bungii*, *Ctenocalanus vanus*, *Heterorhabdus papilliger*, and *Candacia bipinnata*. The common species toward the southern end of the area were *Calanus tenuicornis*, *Nannocalanus minor*, *Neocalanus gracilis*, *N. robustior*, *Eucalanus elongatus*, *Euchaeta spinosa*, *Centropages elongatus*, *Haloptilus longicornis*, *Candacia ethiopica*, *Paracandacia bispinosa*, and *Acartia negligens*. *Euchirella rostrata* was fairly common in the area except at the extreme ends. *Euchaeta media* was common at one station and *Centropages bradyi* at two.

The calculated number of copepods per cubic meter of water varied from 1.1 at station 7 to 110.6 at the northernmost station (table 2). In comparison, Grice (1962) obtained 2.3 to 3.7 calanoids per cubic meter of water for tows at the surface and at 0 to 100 m. in the equatorial Pacific; however, he calculated a mean number of 26.8 copepods per cubic meter of water for depths between about 50 and 150 m. Brodsky (1952) reported a far greater abundance of copepods in the northwestern Pacific—5,040 per cubic meter of water for the 50- to 100-m. level, and 320 for the 100- to 200-m. level.

Of all the previous studies only Brady (1883) and Wilson (1942) reported planktonic copepods from the area under consideration. Brady listed the following nine species of calanoid copepods obtained in a surface plankton sample collected on July 21, 1875, from *Challenger* station 256 (lat. 30°22' N., long. 154°56' W.), which corresponds closely to station 3 of the present collections:

Undinula vulgaris
U. darwini
Euchaeta marina
Pleuromamma abdominalis
Centropages violaceus
Candacia truncata
Labidocera acutifrons
L. detruncata
Pontellopsis villosa

Of these only *Euchaeta marina* and *Centropages violaceus* were in the present collections. Of the remaining species, five were reported from the area by Wilson (1942), and two,

Pleuromamma abdominalis and *Candacia truncata*, were obtained from equatorial waters by Grice (1962).

Wilson (1942) reported 48 species of calanoid copepods in plankton samples collected in early October in 0 to 100-m. tows at *Carnegie* stations 141–145 (between lat. 29°02' N. and lat. 34°06' N., and between long. 145°30' W. and long. 160°44' W.). These stations are in about the same area as the three southern stations of the present collections. Of the 48 species the following 26 were not in the present collections:

Megacalanus longicornis
 **Canthocalanus pauper*
 **Undinula vulgaris*
 **U. darwini*
 **Paracalanus aculeatus*
P. pygmaeus
Acrocalanus gibber
A. gracilis
 **A. longicornis*
Calocalanus styliremis
Microcalanus pusillus
M. pygmaeus
 **Clausocalanus furcatus*
 **Euchirella curticauda*
 **E. pulchra*
Euchaeta acuta
E. tonsa
 **Centropages calaninus*
Lucicutia clausii
 **Haloptilus acutifrons*
 **Candacia simplex*
 **Pontella tenuiremis*
Pontellopsis villosa
 **Labidocera detruncata*
L. acutifrons
L. nerii

Most of these species are tropical or subtropical; 13 species (marked with an asterisk) were found by Grice (1962) in equatorial waters of the Pacific Ocean. If the difference in dates of collection is considered, seasonal changes may account for the absence of many tropical or subtropical copepods in the present collections that were reported in the two previous studies.

SYSTEMATIC ACCOUNT

The copepods were stained with methyl blue in lactic acid and dissected in lactic acid. All illustrations were made with a camera lucida. The total length was measured from the tip of the forehead to the ends of the caudal rami along a sagittal plane. The urosome was measured from the anterior margin of the genital segment to the ends of the caudal rami. These measurements excluded the telescoped portions of the segments. The proportional lengths of the urosomal segments, however, included the telescoped portions.

The anatomical terms used in the descriptions below are defined as follows: Cephalosome—the anterior portion of the body including the first anatomically thoracic segment bearing the maxillipeds. Metasome—the tagma composed of those thoracic segments normally bearing swimming legs; that is, the second to sixth anatomically thoracic segments. Prosome—the cephalosome and metasome, thus, the portion of the body anterior to the major articulation. Urosome—the portion of the body posterior to the articulation. In conformity with the prevailing convention, the perianal ring is counted as the last segment. The terminal urosomal structures may be fused into the so-called caudal furca, a complex composed of the perianal ring and the caudal rami, and sometimes an additional urosomal segment.

FAMILY CALANIDAE

Calanus finmarchicus s.l. Jashnov, 1955
(Plate 1, figs. 1–4)

Occurrence

Calanus glacialis

- Sta. 5. 3 adult females, 3.45 to 3.84 mm.
- Sta. 7. 7 adult females, 3.55 to 3.84 mm.
- Sta. 9. 14 adult females, 3.55 to 3.79 mm.; 1 adult male, 3.10 mm.
- Sta. 13. 19 adult females, 3.69 to 4.30 mm.; 2 adult males, 3.63 to 3.66 mm.
- Sta. 15. 13 adult females, 3.40 to 3.84 mm.; 7 adult males, 3.20 to 3.70 mm.

Sta. 16. 1 adult female, 3.40 mm.

Calanus pacificus

- Sta. 13. 6 adult females, 2.80 to 3.00 mm.
- Sta. 15. 18 adult females, 2.73 to 3.01 mm.; 3 adult males, 2.67 to 2.80 mm.
- Sta. 16. 18 adult females, 2.62 to 2.97 mm.; 8 adult males, 2.64 to 2.87 mm.

Remarks

C. finmarchicus s. 1. has been extensively studied by Jashnov (1955, 1957a, 1957b, 1958, 1961), Brodsky (1948, 1950, 1959, 1962, 1965), and Grainger (1961). The specimens in the present collections can be divided into two size groups. The large form is identified with *C. glacialis* Jashnov, 1955, and the small form is probably referable to *C. pacificus* Brodsky, 1948.

C. glacialis is an arctic species, widely distributed in the polar basin and marginal seas (Jashnov, 1955; Grainger, 1961). This species has also been reported from the Sea of Okhotsk by Ponomareva (1961) but has not been previously recorded from the open Pacific Ocean.

The female of *C. glacialis* has a total length of 3.40 to 4.30 mm. The proportional lengths of the prosome and the urosome are about 3.5–3.7:1. The genital segment is wider than long (53:47), and the caudal ramus is 1.4 times longer than wide (fig. 1). The inner margin of the coxa of the fifth leg has a conspicuous concavity and 17 to 29 teeth (fig. 2). The third endopodal segment of the fifth leg has 5 or 6 setae.

The total length of female *C. pacificus* varies from 2.62 to 3.01 mm. The proportional lengths of the prosome and the urosome are about 3.28–3.47:1. The genital segment is slightly longer than wide (51:49), and the caudal ramus 1.6 times as long as wide (fig. 3). The coxa of the fifth leg has a conspicuous concavity and 24 to 36 teeth along the inner margin (fig. 4). The distal segment of the endopod of the fifth leg has 5 or 6 setae as does that of *C. glacialis*.

The males of the two forms are also readily distinguished from each other by size. Males of *C. glacialis* are 3.10 to 3.70 mm., those of *C. pacificus* 2.64 to 2.87 mm.

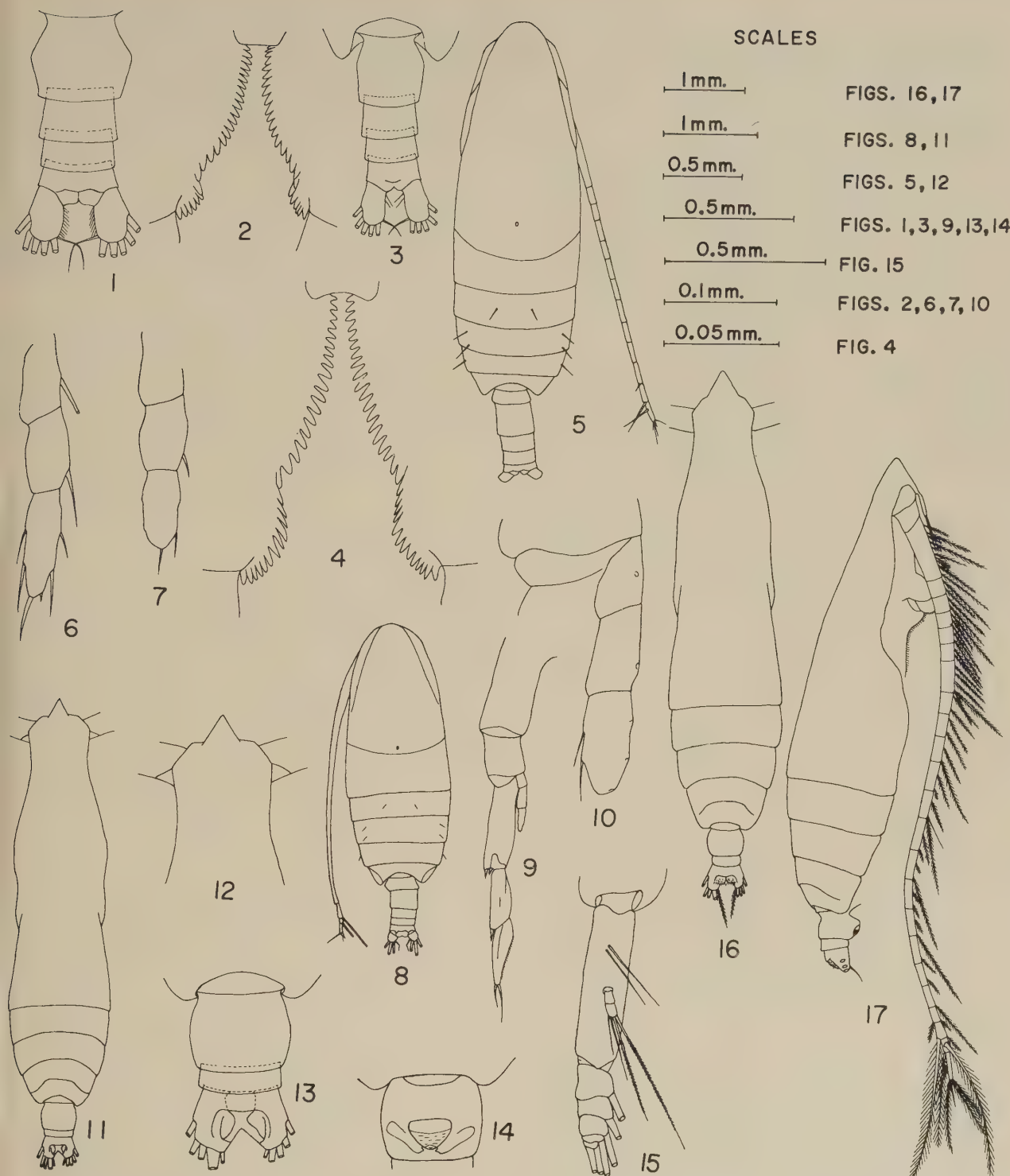


PLATE 1.—Figs. 1–2, *Calanus glacialis*. Female: fig. 1, urosome, dorsal view; fig. 2, inner margins of coxae of fifth pair of legs. Figs. 3–4, *Calanus pacificus*. Female: fig. 3, urosome, dorsal view; fig. 4, inner margins of coxae of fifth pair of legs. Figs. 5–7, *Neocalanus gracilis*. Male: fig. 5, habitus, dorsal view; figs. 6–7, endopods of left fifth legs. Figs. 8–10, *Neocalanus robustior*. Male: fig. 8, habitus, dorsal view;

fig. 9, left fifth leg; fig. 10, endopod of left fifth leg. Figs. 11–15, *Eucalanus attenuatus*, small form. Female: fig. 11, habitus, dorsal view; fig. 12, forehead, dorsal view; fig. 13, urosome, dorsal view; fig. 14, genital segment, ventral view; fig. 15, mandibular palp. Figs. 16–17, *Eucalanus attenuatus*, large form. Female: fig. 16, habitus, dorsal view; fig. 17, habitus, lateral view.

The distal portions of the swimming legs were missing in all specimens.

Calanus tenuicornis Dana, 1849

Occurrence

- Sta. 3. 10 adult females, 1.71 to 1.83 mm.
Sta. 5. 17 adult females, 1.68 to 2.04 mm.; 1 adult male, 1.88 mm.
Sta. 7. 13 adult females, 1.78 to 2.22 mm.
Sta. 9. 2 adult females, 1.90 to 1.98 mm.
Sta. 13. 5 adult females, 1.88 to 2.22 mm.
Sta. 15. 1 adult female, 1.91 mm.

Remarks

This species can easily be recognized by the elongate antennules and the absence of the hooked spiniform process on the anterior aspect of the basis of the first leg that appears in the species of *Neocalanus*.

Most of the present specimens, like those observed by Bowman (1955) and Grice (1962), had protozoan parasites in the caudal rami and the setae were consequently eroded.

Bowman (1955) found that specimens off the California coast included two different types of *C. tenuicornis* Dana that were distinguishable from each other mainly by their size. He created a new species, *C. lighti*, for the large and elongate form. The present collections have no specimen identifiable with *C. lighti*.

Calanus plumchrus Marukawa, 1921

Occurrence

- Sta. 13. 24 fifth copepodids, 3.93 to 4.41 mm.
Sta. 15. 66 fifth copepodids, 3.84 to 4.03 mm.
Sta. 16. 376 fifth copepodids, 3.84 to 4.32 mm.

Remarks

The specimens of the present collections are identical with the fifth copepodid of *Calanus tonsus* Brady described by Campbell (1934), except that they are smaller than Campbell's (4.5–5.0 mm., from the Strait of Georgia) and have 8 setae, instead of 7, on the third endopodal segment of the third leg.

Tanaka (1956a), who compared adult specimens of *C. plumchrus* from the North Pacific with *C. tonsus* Brady from the Antarctic, reported that the two forms are not identical.

Calanus cristatus Krøyer, 1848

Occurrence

- Sta. 13. 6 fifth copepodids, 6.1 to 6.8 mm.
Sta. 15. 1 fifth copepodid, 6.1 mm.

Nannocalanus minor (Claus, 1863)

Occurrence

- Sta. 3. 14 adult females, 1.70 to 2.20 mm.; 3 adult males, 1.55 to 1.88 mm.
Sta. 5. 75 adult females, 1.84 to 2.24 mm.; 10 adult males, 1.65 to 2.01 mm.
Sta. 7. 21 adult females, 1.81 to 2.07 mm.; 11 adult males, 1.71 to 1.88 mm.
Sta. 9. 15 adult females, 1.84 to 2.04 mm.; 3 adult males, 1.84 to 1.88 mm.
Sta. 13. 1 adult female, 2.21 mm.

Remarks

Sewell (1929) divided females of this species, mainly by size, into two different forms, namely f. *major* and f. *minor*. Later Sewell (1947) also recognized two forms of the male. I was unable to distinguish these forms among the present specimens.

Neocalanus gracilis (Dana, 1849)

(Plate 1, figs. 5–7)

Occurrence

- Sta. 3. 8 adult females, 3.00 to 3.20 mm.
Sta. 5. 30 adult females, 3.16 to 3.46 mm.; 7 adult males, 2.80 to 2.83 mm.
Sta. 7. 16 adult females, 3.26 to 3.55 mm.; 5 adult males, 2.73 to 2.93 mm.
Sta. 9. 47 adult females, 3.26 to 3.74 mm.; 3 adult males, 2.83 to 3.06 mm.
Sta. 13. 6 adult females, 3.45 to 3.64 mm.

Remarks

In the male, the first metasomal segment is separate from the cephalosome. The distance between a small process on the dorsodistal surface of the cephalosome and the articulation between the cephalosome and the first meta-

somal segment is nearly equal to the length of the first metasomal segment (fig. 5). The endopod of the left fifth leg (fig. 6) is not as well developed as that of the fourth leg; in some specimens its setae are almost completely reduced (fig. 7).

Neocalanus robustior (Giesbrecht, 1888)
(Plate 1, figs. 8–10)

Occurrence

- Sta. 3. 28 adult females, 4.03 to 4.32 mm.; 7 adult males, 3.16 to 3.45 mm.
Sta. 5. 7 adult females, 4.03 to 4.22 mm.; 11 adult males, 3.36 to 3.45 mm.
Sta. 7. 12 adult females, 4.12 to 4.41 mm.; 3 adult males, 3.36 to 3.55 mm.

Remarks

This species can easily be distinguished from *N. gracilis*—the female by its large size, the shape of the genital segment, and the shape of the external margin of the maxilla, and the male by the location of the small process at the dorsodistal margin of the cephalosome (fig. 8). The left fifth leg of the male (fig. 9) has a rudimentary 3-segmented endopod, the distal segment of which, in some specimens, has 2 or 3 small setae (fig. 10).

FAMILY EUCALANIDAE

Eucalanus attenuatus (Dana, 1849)
(Plate 1, figs. 11–17; plate 2, figs. 1–16; plate 3, figs. 1–13)

Occurrence

Both small and large forms were taken.

Small form

- Sta. 3. 1 adult female, 4.51 mm.;
1 fifth copepodid male, 3.55 mm.
Sta. 5. 2 adult females, 4.51 to 4.70 mm.;
1 fifth copepodid male, 3.64 mm.

Large form

- Sta. 5. 1 fifth copepodid male, 5.56 mm.
Sta. 7. 3 adult females, 6.62 to 6.91 mm.;
1 fifth copepodid female, 5.66 mm.;
4 fifth copepodid males, 5.56 to 6.04 mm.

- Sta. 9. 2 fifth copepodid females, 5.47 to 5.56 mm.;
1 fifth copepodid male, 5.47 mm.
Sta. 13. 5 adult females, 6.52 to 6.81 mm.;
25 fifth copepodid females, 5.56 to 6.14 mm.;
1 adult male, 6.00 mm.;
28 fifth copepodid males, 5.56 to 6.04 mm.
Sta. 15. 11 adult females, 6.52 to 7.00 mm.;
14 fifth copepodid females, 5.47 to 5.95 mm.;
17 fifth copepodid males, 5.56 to 6.04 mm.

The present collections have two forms of *E. attenuatus* differing from each other mainly in size of the body and in number of setae of the mandibular palp. The small form seems to agree in anatomical details with the description given by Giesbrecht (1892) to this species, but the large form apparently has not been described. Both forms are described below.

Small Form

The small form is described in less detail than the large form and mainly for comparison.

Description of Female

In a specimen 4.70 mm. long the proportions of the prosome to the urosome are about 7.2:1 (plate 1, fig. 11). Those of the 2 free urosomal segments and the caudal furca are 49:16:35 (plate 1, figs. 13 and 14). The genital segment is wider than long (55:45). The height of the produced, triangular part of the forehead (plate 1, fig. 12) is about four-fifths the length of the base. The mandibular palp (plate 1, fig. 15) has 2 setae on the basis, 4 setae on the second endopodal segment, and 6 setae on the exopod.

Description of Immature Male

Only 2 fifth copepodid males were found. These immature forms can readily be identified by the setal arrangement on the mandible, which is the same as that of the adult female.

Large Form

Detailed descriptions of adult females, fifth copepodid female, adult male, and fifth copepodid male follow.

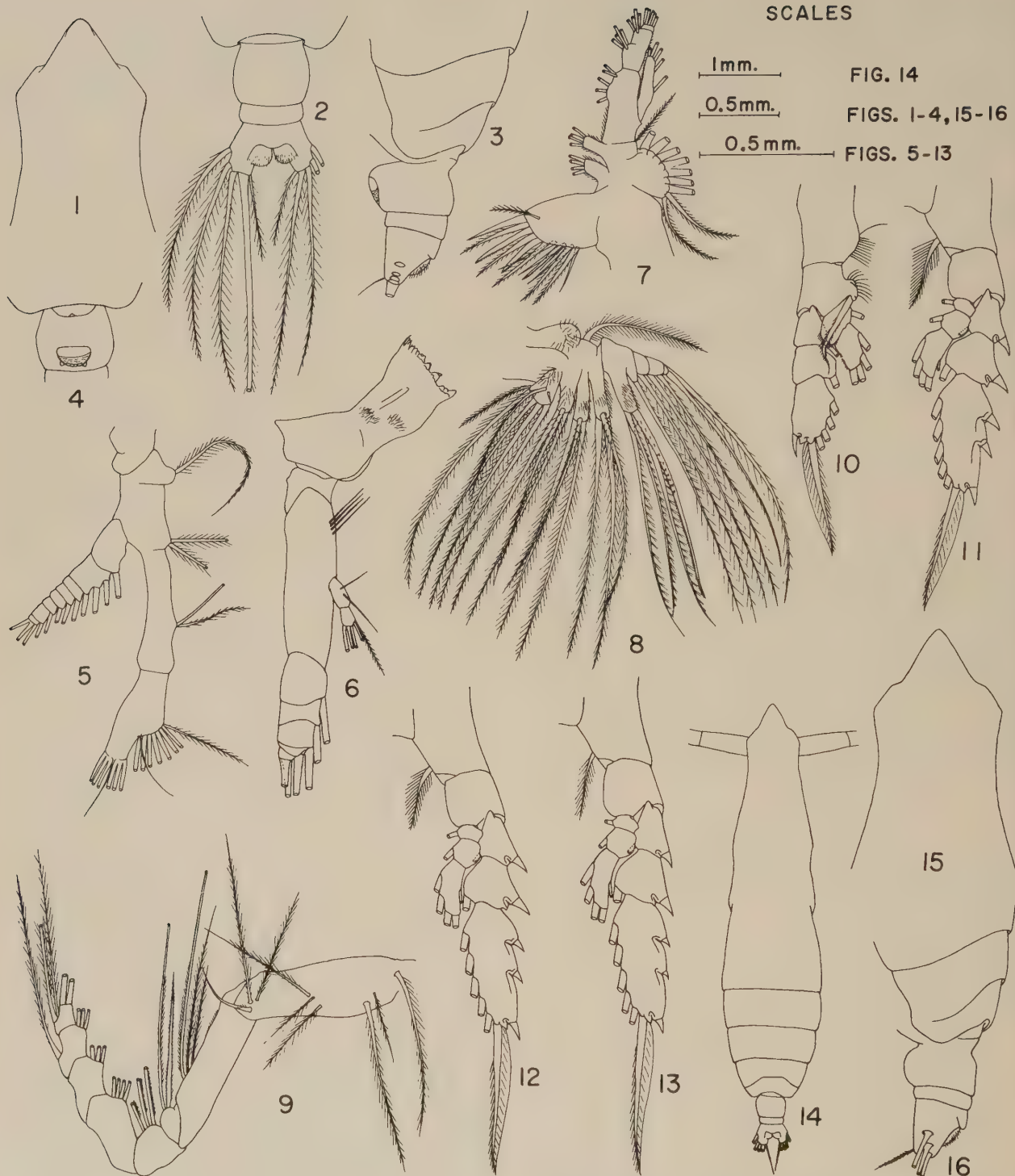


PLATE 2. Figs. 1-16, *Eucalanus attenuatus*, large form. Female: fig. 1, forehead, dorsal view; fig. 2, urosome, dorsal view; fig. 3, posterior part of metasome and urosome, lateral view; fig. 4, genital segment, ventral view; fig. 5, antenna; fig. 6, mandible; fig. 7,

maxillule; fig. 8, maxilla; fig. 9, maxilliped; fig. 10, first leg; fig. 11, second leg; fig. 12, third leg; fig. 13, fourth leg. Fifth copepod females: fig. 14, habitus, dorsal view; fig. 15, forehead, dorsal view; fig. 16, posterior part of metasome and urosome, lateral view.

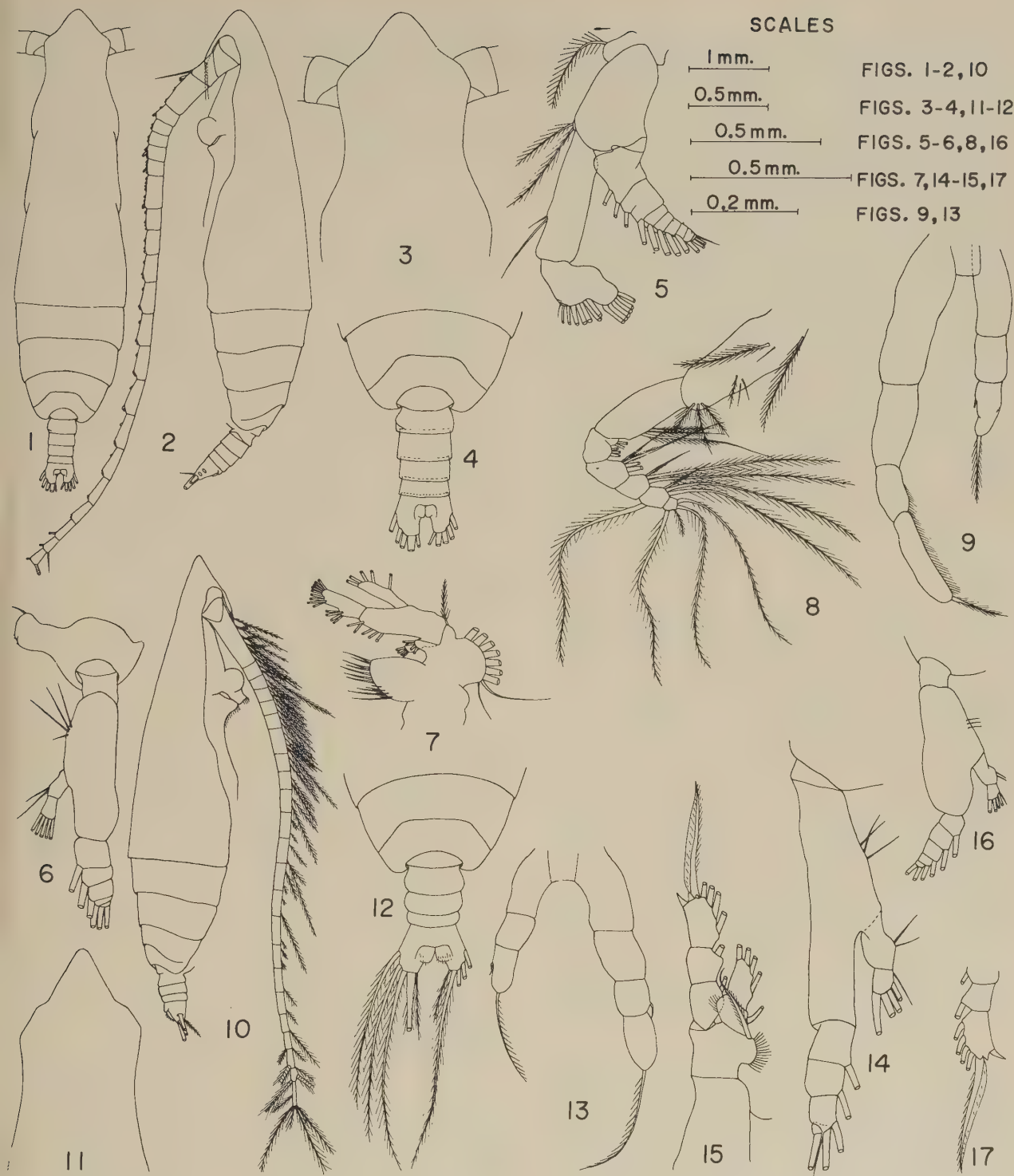


PLATE 3. Figs. 1-13, *Eucalanus attenuatus*, large form. Male: fig. 1, habitus, dorsal view; fig. 2, habitus, lateral view; fig. 3, forehead, dorsal view; fig. 4, posterior part of metasome and urosome, dorsal view; fig. 5, antenna; fig. 6, mandible; fig. 7, maxillule; fig. 8, maxilliped; fig. 9, fifth pair of legs. Fifth copepodid

male: fig. 10, habitus, lateral view; fig. 11, forehead, dorsal view; fig. 12, posterior part of metasome and urosome, dorsal view; fig. 13, fifth pair of legs. Figs. 14-17, *Eucalanus elongatus*. Female: fig. 14, mandibular palp; fig. 15, first leg. Male: fig. 16, mandibular palp; fig. 17, exopod of first leg.

Description of Adult Female

The total lengths of 19 adult females range from 6.52 to 7.00 mm. The prosome is much longer than the urosome (plate 1, fig. 16), and the ratio of these two body parts is about 7.6:1. The anterior region of the head (plate 2, fig. 1) is markedly constricted in front of the antennules and is triangular in dorsal view; the height is about two-thirds the length of the base. The first metasomal segment is fused with the cephalosome. The fourth and fifth metasomal segments are not completely separated, but are fused in the ventrolateral regions (plate 2, fig. 3). The posterolateral corners of the metasome are smoothly rounded.

The urosome consists of 2 free segments and the compound caudal furca. The first or genital segment is composed of 2 fused segments, and the caudal furca is formed of 2 segments fused with the rami. The proportional lengths of the segments and caudal furca, from anterior to posterior, are 45:18:37.

The genital segment (plate 2, fig. 2) is wider than long (55:45); ventrally it projects in a round swelling, bearing the genital aperture (plate 2, figs. 3 and 4). The left caudal ramus is slightly larger than the right. The second medial terminal seta on the left ramus is markedly stouter and much longer than the others.

The antennule (plate 1, fig. 17) has 23 free segments; the first and second and the eighth and ninth segments are fused. The last 6 segments extend beyond the caudal rami. Each segment carries one or several strong plumose setae that are often reddish.

The exopod of the antenna (plate 2, fig. 5) is 8-segmented, has 12 setae, and reaches about the end of the first endopodal segment. The first endopodal segment is about 1.3 times as long as the second and has 2 setae along the inner edge, two-fifths the length of the segment from the distal end. The second endopodal segment has 8 long setae and 1 short seta on the internal lobe and 6 long setae and 1 short seta on the external lobe.

The mandibular palpus (plate 2, fig. 6) is 1.7 times as long as the mandibular blade and is biramous. The basis is more or less cylindrical and has 4 setae at the upper portion of the internal margin. The endopod arises from near

the middle of the basis and is 2-segmented; the first segment has 2 short setae and the second 1 short seta and 4 long setae.

In the maxillule (plate 2, fig. 7), the first inner lobe has 15 spines, and each of the second and third inner lobes has 4 setae. The first outer lobe is rather small and has 9 setae. The second outer lobe is not pronounced and has a single plumose seta. The basis has 5 setae along the internal margin and carries laterally an exopod and distally an endopod. The exopod has 5 setae. The endopod is 3-segmented; the first 2 segments are partially fused and each has 4 setae, and the small apical segment has 5 setae.

The maxilla (plate 2, fig. 8) is well developed. The outer margin of the coxa has a round swelling with hairs. Next to the swelling is a markedly depressed portion from which arises a long, plumose seta. The various lobes are well developed. The first lobe has 6 setae and a small spine, each of the second to fourth lobes has 3 setae, the fifth lobe carries 3 setae and a long spine, and the sixth lobe has a single seta. In addition, the segments of the endopod have setae as follows: 1 on the first, 2 on the second, and 2 on the terminal segment.

The coxa of the maxilliped (plate 2, fig. 9) is composed of 4 lobes: the proximal lobe has 1 seta; the second, 2 setae; and the third and fourth lobes, 3 setae each. The basis has 3 setae just distad of the midpoint and 2 on the distal lobe. The endopod consists of 5 segments, which have 3, 4, 3, 3 + 1, and 2 + 2 setae, respectively.

The coxa of the first leg (plate 2, fig. 10) lacks setae, but its inner margin is fringed with hairs. The basis has a curved, plumose seta at the internal apex. The exopod is 3-segmented. The first and second segments are devoid of external spines, but each has 1 internal seta; the third segment has 1 external spine at the distal corner, a slender terminal spine, and 4 internal setae. The endopod is 2-segmented: the first segment has a single internal seta; the second segment 2 internal and 2 terminal setae.

The second to fourth legs (plate 2, figs. 11-13) are alike. The coxa has an internal plumose seta, but the basis lacks setae. Both the exopod and the endopod are 3-segmented. Each of the first and second exopodal segments has 1 strong external spine and 1 internal seta; the third

segment has 3 external spines, 5 internal setae, and 1 slender terminal spine. Each of the first and second endopodal segments has 1 internal seta. The third segment has 1 external seta, 2 internal setae, and 2 terminal setae. The fifth pair of legs is lacking.

Description of Fifth Copepodid Female

The total lengths of 42 specimens range from 5.47 to 6.14 mm. The prosome is about 7.8 times as long as the urosome. The body shape (plate 2, figs. 14 and 15) resembles that of the adult female. The genital segment shows a distinct ventral swelling (plate 2, fig. 16), but is not so strongly swollen as that of the adult female, and lacks the genital opening.

The segmental composition of the antennule is exactly like that of the adult female. The setal arrangement appears to be the same. The antennae, masticatory appendages, and the swimming legs are all similar to those of the adult female, but the internal lobe of the second endopodal segment of the antenna has 7 long setae instead of 8; and the second to fourth endopodal segments of the maxilliped have 3, 2, and 3 setae instead of 4, 3, and 4.

Description of Adult Male

The adult male was described from a single specimen. The total length is 6.00 mm.; the ratio of the prosome to the urosome is about 6:1. The forehead in dorsal view (plate 3, figs. 1 and 3) is almost triangular, but the apex is smoothly rounded and much less produced than in the adult female. The first metasomal segment is fused with the cephalosome. The fourth and fifth metasomal segments are not completely separated, but are fused in the ventrolateral regions (plate 3, fig. 2). The posterolateral corners of the metasome are smoothly rounded.

The urosome (plate 3, fig. 4) consists of 4 free segments and the caudal furca, a complex composed of the anal segment fused with the caudal rami. The segments and caudal furca have the following proportional lengths, from anterior to posterior: 17:22:18:13:30.

The genital segment is slightly produced on the left side, and has a distinct genital operculum. The left caudal ramus is slightly larger than the right. The second medial terminal seta

on the left ramus is markedly stouter and much longer than the others.

The antennule (plate 3, fig. 2) has 24 free segments, only the eighth and ninth of which are fused; the last 7 segments extend beyond the caudal furca. The antenna (plate 3, fig. 5) is very similar to that of the female but the basis is stouter.

The mandible (plate 3, fig. 6) differs from that of the female in two respects: it is smaller, and the mandibular blade is degenerated and has a single spinelike tooth. The basis has 4 setae at the upper portion of the internal margin, as does that of the female. The endopod arises just distad of the midpoint of the basis and has 2 setae on the first segment and 5 on the second segment.

The maxillule (plate 3, fig. 7), maxilla, and the maxilliped (plate 3, fig. 8) are much smaller than those of the adult female but resemble the latter in shape and in details of setal arrangement.

The first to fourth pairs of legs are nearly identical with those of the female. The left and right fifth legs (plate 3, fig. 9) are both uniramous. The left one is 4-segmented; the distal segment is tipped with a seta, and the last two segments are fringed with hairs along the inner margins. The segments in the left fifth leg have the proportional lengths of 39:21:14:26. The right fifth leg is also 4-segmented, but the last 2 segments are incompletely separated. The distal segment is tipped with a seta, and the third segment has a small spine on its inner edge. The right fifth leg is short—it reaches about the middle of the second segment of the left leg. The segments have the proportional lengths of 48:24:28 (third + fourth).

Description of Fifth Copepodid Male

The total length of 51 specimens ranges from 5.47 to 6.04 mm. The proportional lengths of the prosome and urosome are 7.7:1. The general body shape (plate 3, fig. 10) resembles that of the fifth copepodid female. The head in dorsal view (plate 3, fig. 11) has a triangular frontal part that ends in a blunt point. The urosome (plate 3, fig. 12) consists of 3 free segments and the caudal furca.

The antennule (plate 3, fig. 10) has 23 free

segments. The first and second and the eighth and ninth segments are fused, as in the adult female and fifth copepodid female. The antennae, masticatory appendages, and the first to fourth pairs of legs are identical with those of the fifth copepodid female. The fifth pair of legs (plate 3, fig. 13) is not fully developed. The left one is 4-segmented; the third segment carries a small outer spine, and the distal segment is tipped with a long seta. The right fifth leg is 3-segmented; the distal segment is tipped with a long seta and has a small external spine.

Remarks

The two forms of *E. attenuatus* closely resemble each other in general anatomy but are clearly distinct in size of the body and in setation of the mandibular palp. The total length of the adult female is 4.51 to 4.70 mm. in the small form and 6.52 to 7.00 mm. in the large form. The mandibular palp of the large form has 4 setae on the basis, 2 setae on the first endopodal segment, and 5 setae on the second; the palp of the small form has 2 setae on the basis, no seta on the first endopodal segment, and 4 setae on the second.

The biological significance of the morphological differences shown by the large form cannot be evaluated on the basis of the materials on hand. A. Fleminger (personal communication), however, regards the large forms as ecophenotypic variants.

Eucalanus elongatus (Dana, 1849) (Plate 3, figs. 14-17)

Occurrence

- Sta. 3. 10 adult females, 5.95 to 6.40 mm.
- Sta. 5. 17 adult females, 6.24 to 6.91 mm.;
1 fifth copepodid male, 4.80 mm.
- Sta. 7. 23 adult females, 6.05 to 7.00 mm.;
1 adult male, 4.60 mm.
- Sta. 13. 9 adult females, 6.14 to 6.72 mm.;
1 adult male, 4.70 mm.;
13 fifth copepodid males, 4.60 to 4.90 mm.
- Sta. 15. 3 adult females, 6.30 to 6.70 mm.;
4 fifth copepodid males, 4.70 to 4.80 mm.

Remarks

Giesbrecht (1892) described three varieties of *E. elongatus*, namely, *hyalinus*, *inermis*, and *bungii*. Johnson (1938) raised *inermis* and *bungii* to the status of species. The specimens listed here are identical with *hyalinus* and are mainly characterized by the pointed posterolateral corners of the metasome. The mandible has 3 short setae on the proximal part of the basis and 4 long setae plus 1 short seta on the second endopodal segment (figs. 14 and 16). The third exopodal segment of the first leg has 1 external spine (figs. 15 and 17).

Eucalanus bungii Giesbrecht, 1892 (Plate 4, figs. 1-3)

Occurrence

E. bungii bungii Johnson, 1938

- Sta. 16. 19 adult females, 5.51 to 6.08 mm.;
3 fifth copepodid females, 4.27 to 4.75 mm.;
4 fifth copepodid males, 4.27 to 4.56 mm.

E. bungii californicus Johnson, 1938

- Sta. 5. 1 fifth copepodid female, 4.22 mm.;
1 fifth copepodid male, 4.12 mm.
- Sta. 7. 4 adult females, 5.66 to 5.95 mm.;
3 fifth copepodid females, 4.22 to 4.51 mm.;
6 fifth copepodid males, 4.12 to 4.51 mm.
- Sta. 13. 7 adult females, 5.70 to 6.40 mm.;
20 fifth copepodid females, 4.30 to 4.80 mm.;
22 fifth copepodid males, 4.00 to 4.30 mm.
- Sta. 15. 20 adult females, 5.28 to 6.40 mm.;
2 fifth copepodid males, 4.20 to 4.40 mm.
- Sta. 16. 4 adult females, 5.70 to 6.27 mm.

Remarks

Eucalanus bungii can be easily distinguished from *E. elongatus* by the rounded postero-

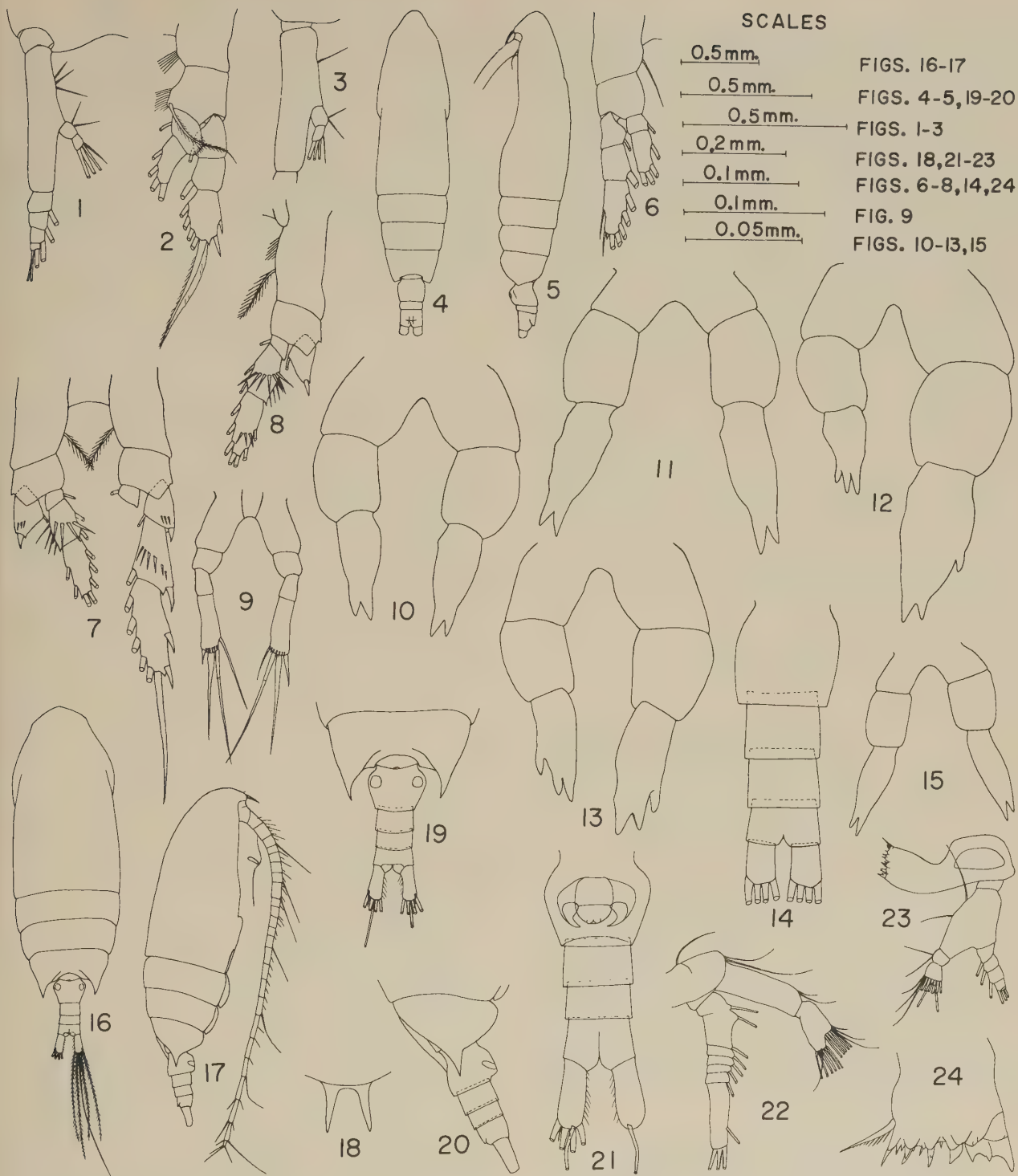


PLATE 4. Figs. 1-3, *Eucalanus bungii*. Female: fig. 1, mandibular palp (*E. bungii bungii*); fig. 2, first leg (*E. bungii bungii*); fig. 3, mandibular palp (*E. bungii californicus*). Figs. 4-9, *Calocalanus tenuis*. Female: fig. 4, habitus, dorsal view; fig. 5, habitus, lateral view; fig. 6, first leg; fig. 7, second pair of legs; fig. 8, third leg; fig. 9, fifth pair of legs. Figs. 10-13, *Clausocalanus arcuicornis*. Female: fig. 10, fifth pair of legs, large form; fig. 11, fifth pair of legs, small

form; figs. 12-13, abnormal fifth pairs of legs. Figs. 14-15, *Clausocalanus pergens*. Female: fig. 14, urosome, dorsal view; fig. 15, fifth pair of legs. Figs. 16-24, *Aetideus pacificus*. Female: fig. 16, habitus, dorsal view; fig. 17, habitus, lateral view; fig. 18, rostrum; fig. 19, posterior part of metasome and urosome, dorsal view; fig. 20, *idem*, lateral view; fig. 21, urosome, ventral view; fig. 22, antenna; fig. 23, mandible; fig. 24, cutting edge of mandibular blade.

lateral margins of the last metasomal segment and the presence of 2 external spines on the terminal exopodal segment of the first leg (fig. 2). By the setation of the mandibular palp, the specimens of the present collections can be divided into two forms that Johnson (1938) described as subspecies—*E. bungii bungii*, which has 3 setae on the basis of the palp (fig. 1), and *E. bungii californicus*, which has a single seta on this structure (fig. 3). Since these two forms are distinguishable from each other only on the basis of this apparently insignificant character, however, it seems better to recognize them as ecophenotypic variants than as subspecies.

Finding all possible transitions between Giesbrecht's (1892) varieties *hyalinus* and *bungii* in the *Snellius* plankton samples, Vervoort (1946) disagreed with Johnson's (1938) idea of elevating these varieties to specific level. The present materials, however, are in favor of Johnson's (1938) treatment in the absence of any intermediate forms.

Mecynocera clausii Thompson, 1888

Occurrence

- Sta. 5. 4 adult females, 1.05 to 1.08 mm.;
1 fifth copepodid male, 0.99 mm.
- Sta. 7. 5 adult females, 1.05 to 1.15 mm.;
2 fifth copepodid males, 0.99 mm.
- Sta. 9. 1 adult female, 1.08 mm.

Remarks

This species can be recognized by the exceptionally long antennule, which is about twice as long as the body, and the comparatively small size of the copepod itself. According to T. Scott (1894), the fifth leg in both sexes of this species is 5-segmented. The three males in the present collections have 4-segmented fifth legs and 4-segmented urosomes, indicating that they are immature.

FAMILY PARACALANIDAE

Paracalanus parvus (Claus, 1863)

Occurrence

- Sta. 13. 1 adult female, 1.00 mm.

Remarks

I find it curious that we took only one specimen of this reportedly cosmopolitan species.

Calocalanus pavo (Dana, 1849)

Occurrence

- Sta. 5. 2 adult females, 1.08 to 1.12 mm.
- Sta. 7. 10 adult females, 1.05 to 1.18 mm.

Remarks

Although widely distributed in the tropical and subtropical regions of all three great oceans, this species was found at only two of the stations.

Calocalanus tenuis Farran, 1926
(Plate 4, figs. 4-9)

Occurrence

- Sta. 13. 4 adult females, 1.15 to 1.24 mm.

Description of Female

The body (figs. 4 and 5) is slender and fusiform; the anterior end of the cephalosome is vaulted. The cephalosome and the first metasomal as well as the fourth and fifth metasomal segments are completely fused. The urosome consists of 3 free segments and the caudal rami. The segments and caudal rami have the following proportional lengths, from anterior to posterior: 38:15:32:15. The genital segment is slightly broader than long in the proportions of 56:44. The caudal ramus is about as broad as it is long.

The first leg (fig. 6) has a 3-segmented exopod and a 2-segmented endopod. The coxa has a seta on the internal margin. The exopod has 0, 0, 2 external spines, 1, 1, 4 internal setae, and a terminal seta. The endopod has 1, 2 internal setae and 2 terminal setae.

The second leg (fig. 7) carries a plumose seta on the internal margin of the coxa. The 3-segmented endopod has 1, 2, and 7 setae, respectively. There are 4 spines, in a transverse row, on the posterior surface and 4 spines on the external margin of the second endopodal segment. The exopod is also 3-segmented, with 1, 1, 2 external spines and 1, 1, 5 internal setae in addition to a terminal seta. The posterior surfaces of the first and second exopodal segments carry 3 and 6 spines, respectively.

The endopod of the third leg (fig. 8) is 3-segmented. The segments have 1, 2, 7 setae, as does the endopod of the second leg. In addition, the second segment has 6 spines on the posterior surface and 4 spines on the external

margin, and the third segment has 3 small spines on the posterior surface.

The fifth leg (fig. 9) is uniramous and 4-segmented. The segments have the proportional lengths of 35:13:17:35. The fourth segment has 1 distally situated external spine, 1 terminal spine, 2 distally situated internal setae, and a row of spinules at the bases of these spines and setae. As shown in figure 9, the right and left legs are different in the lengths of the external spines and the upper internal setae.

Remarks

Calocalanus tenuis was first described from the Bay of Biscay by Farran (1926); it has not been reported from the Pacific. The specimens in the present collections are poor, because some appendages are broken off. They are, however, readily recognized by the slender, fusiform body and the characteristic shape of the fifth leg.

FAMILY PSEUDOCALANIDAE

Pseudocalanus minutus (Kroyer, 1848)

Occurrence

Sta. 16. 1 adult female, 1.26 mm.

Clausocalanus arcuicornis (Dana, 1849) (Plate 4, figs. 10-13)

Occurrence

Sta. 3. 7 large females, 1.51 to 1.60 mm.;
14 small females, 1.38 to 1.48 mm.;
2 males, 1.40 mm.

Sta. 5. 4 large females, 1.51 to 1.58 mm.;
3 small females, 1.12 to 1.41 mm.;
1 male, 1.28 mm.

Sta. 7. 6 large females, 1.50 to 1.55 mm.;
5 small females, 1.12 to 1.46 mm.

Sta. 9. 4 large females, 1.58 to 1.70 mm.;
3 small females, 1.28 to 1.50 mm.;
1 male, 1.42 mm.

Sta. 13. 7 large females, 1.65 to 1.83 mm.;
20 small females, 1.37 to 1.58 mm.;
1 male, 1.23 mm.

Sta. 15. 5 large females, 1.68 to 1.83 mm.;
21 small females, 1.20 to 1.51 mm.;
1 male, 1.14 mm.

Sta. 16. 5 small females, 1.28 to 1.31 mm.;
1 male, 1.46 mm.

Remarks

Sewell (1929), who studied material from the Indian Seas, divided females of *C. arcuicornis* into two forms, namely f. *minor* and f. *major*, mainly differing in the structure of the fifth pair of legs and the proportional lengths of the prosome and urosome. Grice (1962) found two female forms of this species in the equatorial Pacific and tentatively identified these with the two forms described by Sewell (1929). The females of the present collection also fall into two groups that are separable mainly by the total lengths and the shapes of the fifth pairs of legs.

The total lengths of the large form range from 1.50 to 1.83 mm. The prosome is 2.7 to 3.1 times as long as the urosome. In the fifth leg (fig. 10), the proximal segment is stouter and is longer than or as long as the following segment, and the terminal segment is shorter than the preceding two segments combined. The general shape of the fifth pair of legs is similar to that of f. *major* described by Sewell (1929), but my specimens are much larger than the 1.17 mm. reported by him.

The total length of the small form is 1.12 to 1.58 mm. The proportional lengths of the prosome and urosome are about equal to those in the large form. The proximal segment of the fifth leg (fig. 11) is slightly narrower and is shorter than the following segment. The terminal segment is longer than or as long as the preceding two segments combined. This small form seems to correspond to f. *major* described by Grice (1962) in total length and shape of the fifth pair of legs, but is not identical with Sewell's *major* in shape of the fifth pair of legs.

Two females from station 9 had abnormal fifth pairs of legs (figs. 12 and 13).

Clausocalanus pergens Farran, 1926 (Plate 4, figs. 14 and 15)

Occurrence

Sta. 7. 1 adult female, 0.85 mm.

Sta. 13. 1 adult female, 0.94 mm.

Remarks

This species can be distinguished from *C.*

arcuicornis mainly by its smaller size and other, minor, differences. The prosome is 2.5 to 2.8 times as long as the urosome. The caudal ramus (fig. 14) is longer than wide (63:37). The segments of the fifth leg (fig. 15) have the proportional lengths of 21:29:50, from proximal to distal.

Ctenocalanus vanus Giesbrecht, 1888

Occurrence

- Sta. 5. 2 adult females, 1.06 to 1.08 mm.
- Sta. 7. 6 adult females, 1.08 to 1.13 mm.
- Sta. 9. 2 adult females, 1.14 mm.
- Sta. 13. 4 adult females, 1.08 to 1.17 mm.
- Sta. 15. 1 adult female, 1.26 mm.
- Sta. 16. 5 adult females, 1.26 to 1.28 mm.;
5 fifth copepodid males, 1.26 to 1.28 mm.

Remarks

This species was at all the stations except the southernmost, although not in large numbers. It can easily be recognized by the ctenoid form of the external spines of the third exopodal segment of the third and fourth legs.

FAMILY AETIDEIDAE

Aetideus pacificus Brodsky, 1950

(Plate 4, figs. 16-24; plate 5, figs. 1-7)

Occurrence

- Sta. 16. 5 adult females, 2.21 to 2.30 mm.

A complete description is given here because Brodsky's original description is brief and seems to disagree in some anatomical details with the present specimens.

Description of Female

The total lengths of five adult females range from 2.21 to 2.30 mm. The prosome is about 3.4 times as long as the urosome. The general outline of the prosome is ovate. In dorsal aspect the greatest width is at the fusion of the cephalosome and the first metasomal segment (plate 4, fig. 16). The first metasomal segment is completely fused with the cephalosome. The fourth and fifth metasomal segments are also completely fused. The cephalosome in dorsal aspect is slightly dilated in the oral region and is smoothly rounded anteriorly. The rostrum

consists of two rather slender processes (plate 4, fig. 18).

The posterolateral corners of the metasome are produced into acute points, which in dorsal view are slightly curved inward (plate 4, fig. 19) and in lateral aspect point straight backward (plate 4, fig. 20). These points do not reach the distal margin of the genital segment in either dorsal or lateral view.

The urosome (plate 4, figs. 19-21) is 4-segmented; the segments and the caudal rami have the following proportional lengths, from anterior to posterior: 31:17:14:13:25. The genital segment in dorsal aspect is slightly wider than long (29:25) and has broadly rounded sides. The caudal rami are about 2.5 times as long as broad, and have 4 terminal setae of subequal length, a long ventral seta that is longer than the terminal setae, and a short external seta.

The antennule is 24-segmented; when it is applied against the body, its last 2 segments extend beyond the end of the caudal ramus (plate 4, fig. 17).

The endopod of the antenna (plate 4, fig. 22) is slightly shorter than the exopod. The first endopodal segment is styliform and has 2 setae almost at the distal end of the internal margin. The second endopodal segment is about half the length of the first and has 6 + 1 setae on the external lobe and 8 setae on the internal lobe. The first and second exopodal segments are incompletely separated; the former has no setae, but the latter has 2 setae proximally along the internal margin and 1 seta at the distal end of that margin. The third to sixth segments are fully separated; each has a strong seta. The seventh segment is elongate and has an internal seta at about two-thirds the length of the segment from the proximal end, and 3 apical setae.

The mandibular palp (plate 4, fig. 23) has a squarish basis with 2 setae along the internal margin. The endopod is 2-segmented and has 2 setae on the first segment and 9 + 2 on the second. The exopod is 5-segmented; each of the proximal 4 segments has a strong seta, and the distal segment 2 apical setae. The cutting edge of the mandibular blade (plate 4, fig. 24) is armed with about six groups of teeth and a basal seta.

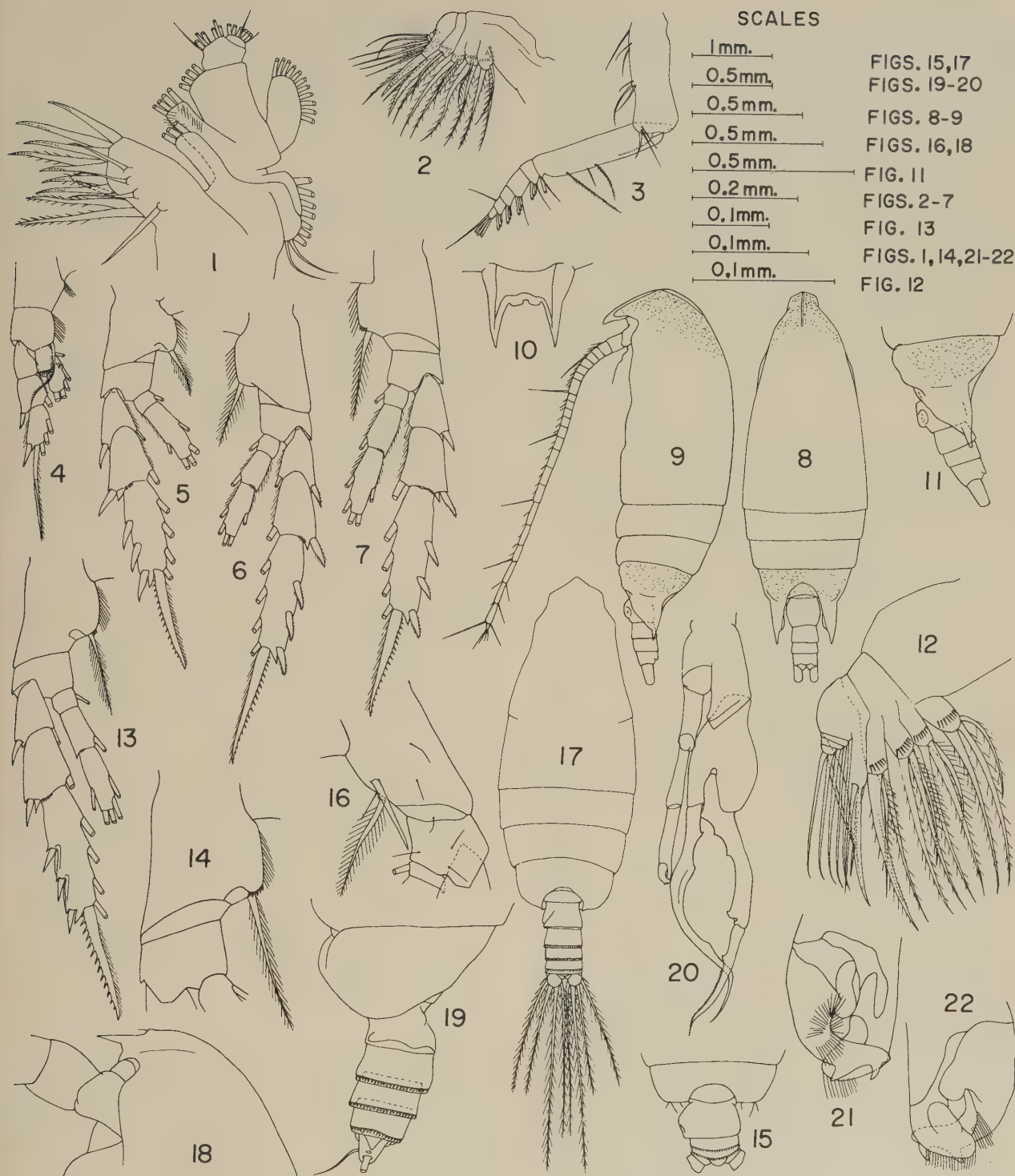


PLATE 5. Figs. 1-7, *Aetideus pacificus*. Female: fig. 1, maxillule; fig. 2, maxilla; fig. 3, maxilliped; fig. 4, first leg; fig. 5, second leg; fig. 6, third leg; fig. 7, fourth leg. Figs. 8-14, *Euaetideus acutus*. Female: fig. 8, habitus, dorsal view; fig. 9, habitus, lateral view; fig. 10, rostrum; fig. 11, posterior part of metasome and urosome, lateral view; fig. 12, maxilla; fig. 13, fourth leg; fig. 14, basipod of fourth leg. Figs.

15-22, *Euchirella truncata*. Female: fig. 15, posterior part of metasome and urosome, dorsal view; fig. 16, basipod of fourth leg. Male: fig. 17, habitus, dorsal view; fig. 18, forehead, lateral view; fig. 19, posterior part of metasome and urosome, lateral view; fig. 20, fifth pair of legs, posterior aspect; fig. 21, terminal part of left fifth leg, posterior aspect; fig. 22, *idem*, anterior aspect.

The maxillule (plate 5, fig. 1) is well developed. The first inner lobe has 9 strong spines along the internal margin, 4 relatively small spines on the posterior surface, and 1 small spine on the anterior surface. The second and third inner lobes are elongate and have 3 and 4 setae, respectively. The first outer lobe is low and has 9 setae. The basis bears 4 setae at the apex of the internal margin. The exopod has 11 setae. The endopod is 2-segmented, and carries 4 + 3 setae on the first segment and 6 + 2 setae on the second.

The maxilla (plate 5, fig. 2) has 5 well-developed lobes. Each of the first to fourth lobes bears 2 spiniform, spinulose setae of equal length, a short spinulose seta, and a few small spinules near the insertions of the setae. One of the 2 spiniform setae on the fourth lobe is much stouter than the other. The fifth lobe carries a strong dagger-shaped spine in addition to 2 slender setae. The endopod has 6 setae—1 on each of the proximal 3 segments and 3 on the terminal segment.

The maxilliped (plate 5, fig. 3) consists of a long basipod and a short endopod. The coxa has three groups of 3 setae each and is about as long as the basis, which has a row of spinules proximally, 3 scattered setae distally, and 2 setae at the extreme apex. The endopod has 5 segments, which have the following numbers of setae, from proximal to distal: 4, 4, 3, 3 + 1, and 4.

The first pair of legs (plate 5, fig. 4) has 3-segmented exopods and 1-segmented endopods. The coxa has no setae, but bears hairs along the proximal portion of the internal margin. The internal margin of the basis is fringed with hairs and has a curved seta at the distal end. The first exopodal segment lacks setae or spines. The second exopodal segment has an internal seta and an external spine. The internal margin of the spine appears to be slightly denticulate. The third exopodal segment has an external spine with a slightly denticulate internal margin. In addition, the segment has 3 internal setae and a long terminal spine, which has a lamella along the external margin and a row of hairs along the internal margin. Halfway along its external margin the endopod has a round tubercle which has a transverse row of small, acute spinules. In addition, the endopod has 3

internal setae, 2 terminal setae, and some small spinules at the base of the middle internal seta.

The coxa of the second leg (plate 5, fig. 5) has a considerably curved internal margin, which has a row of hairs and a short, thick seta. The basis has no hairs or setae. The exopod is 3-segmented. Each of the first and second segments has an external spine and an internal seta. In anterior aspect a row of small spinules lies along the distal border of the second segment. The third segment has 3 external spines, 4 internal setae, and a dagger-shaped terminal spine armed with 17 triangular teeth. The endopod is 2-segmented, with 1 seta on the first and 5 setae on the second segment, and reaches to about the distal border of the second exopodal segment.

The basipod and exopod of the third leg (plate 5, fig. 6) are similar to those of the second leg, but the external spines of the exopod are fringed with fine hairs and the terminal spine is armed with 19 acute, triangular teeth. The endopod is 3-segmented, with 1 seta on each of the first and second segments and 5 setae on the third, and extends slightly beyond the distal border of the second exopodal segment. A row of very fine spinules lies along the distal border of the second endopodal segment.

The fourth leg (plate 5, fig. 7) differs from the third in the following particulars: About 4 small, acute spines are at the insertion of the seta on the coxa. The endopod is longer, reaching to a line including one-third of the length of the third exopodal segment. The terminal spine is also absolutely shorter, and armed with 18 teeth along the external edge. The fifth pair of legs is absent.

Remarks

The armature of the mandibular blade of the present specimens disagrees with the original description of the species by Brodsky (1950) but agrees with his description for *Aetideus armatus*.

I recently compared female specimens of *A. armatus* and *A. pacificus* from the Pacific coast of North America and found that, although the species are alike in anatomical details of the appendages, they are clearly distinguishable from each other by the size and general shape

of the body. *A. armatus* is 1.80 to 2.02 mm. total length (about 50 specimens) and has metasomal processes that extend beyond the distal end of the genital segment. *A. pacificus*, as described above, has a slender body of 2.20 to 2.43 mm. (seven specimens) and has metasomal processes that do not reach the distal end of the genital segment. The male of *A. pacificus* is not known.

Euaetideus acutus (Farran, 1929)
(Plate 5, figs. 8-14)

Occurrence

- Sta. 3. 3 adult females, 1.65 to 1.68 mm.
Sta. 5. 5 adult females, 1.68 to 1.78 mm.
Sta. 7. 1 adult female, 1.65 mm.
Sta. 9. 1 adult female, 1.68 mm.

Remarks

The female of this species can easily be distinguished by the following characters: The rostrum is very heavy and, in dorsal aspect, distinctly set off from the remainder of the head (fig. 8); the rami (fig. 10) are separated by a deep, U-shaped incision, at the base of which are two small knobs; the posterolateral corners of the metasome are produced into acute points that extend slightly beyond the distal border of the second urosomal segment (fig. 11); the dorsum of the prosome (figs. 8 and 9) has a pitted structure that is particularly visible at the forehead and on the last segment.

The antennae and the mouth parts were figured and described in detail by Vervoort (1957). The present specimens generally agree with his description except for the maxilla. The dagger-shaped spines on the fourth and fifth lobes of the maxilla (fig. 12) are almost identical in diameter, but different in length—the one on the fourth lobe is the longer. Each of the first to fourth lobes has a row of acute spinules, instead of irregular rows of spinules.

The first to fourth pairs of legs in general agree with those figured by Vervoort (1957). Some additional characters in the present specimens are as follows: In stained specimens, a line of demarcation is clearly visible between the first and second endopodal segments of the second leg. A row of fine spinules lies along the

distal border of the second exopodal segment in the second to fourth legs and on the distal border of the second endopodal segment in the third to fourth legs. The coxa of the fourth leg has about 5 acute spinules at the insertion of the internal seta (figs. 13 and 14).

Euchirella truncata Esterly, 1911
(Plate 5, figs. 15-22)

Euchirella truncata Esterly, 1911, p. 322; plate 26, fig. 5; plate 28, fig. 35; plate 29, fig. 63; plate 30, fig. 71; plate 31, fig. 104.

Euchirella propria Esterly, 1911, p. 321, plate 27, figs. 14 and 20; plate 30, figs. 67 and 83; plate 31, fig. 85.

Occurrence

- Sta. 3. 1 adult female, 5.40 mm.
Sta. 5. 5 adult females, 5.56 to 6.06 mm.;
1 adult male, 4.60 mm.
Sta. 7. 5 adult females, 5.85 to 6.24 mm.;
7 adult males, 4.60 to 5.08 mm.
Sta. 9. 2 adult females, 5.71 to 6.14 mm.;
3 adult males, 4.89 to 4.99 mm.
Sta. 13. 1 adult female, 6.81 mm.

Euchirella truncata was originally described by Esterly (1911) from females obtained in the San Diego, Calif., region of the eastern Pacific. As suggested by Vervoort (1963), *Euchirella propria*, erected on males alone by Esterly (1911), seems to be synonymous with *E. truncata*, for in the present study the two forms were found in the same samples and were closely similar in size as well as in anatomical details.

E. truncata has also been recorded from the South Atlantic as *E. gracilis* (Wolfenden, 1911), from the North Atlantic as *E. intermedia* (With, 1915), and from the Gulf of St. Lawrence as *E. acadiana* (Willey, 1919).

Description of Female

The female can easily be recognized by the shape of the genital segment, which is more swollen on the left side (fig. 15), and by the presence of a single strong spine on the coxa of the fourth leg (fig. 16).

Description of Male

The total length ranges from 4.60 to 5.08 mm. The prosome is about 4.2 times as long as the urosome. The cephalosome and the first

metasomal segment as well as the fourth and fifth metasomal segments are fused (fig. 17). The forehead is smoothly rounded and has a strong rostrum (fig. 18). The posterolateral margins of the metasome are rounded (fig. 19).

The urosome consists of 5 free segments and the caudal rami which have the following proportional lengths, from anterior to posterior: 23:22:18:19:6:12. The last segment is almost completely telescoped into the fourth segment. The caudal rami are as long as they are wide. The distal margins of the second to fourth segments are each fringed by a row of small triangular spinules.

The uniramous left fifth leg (fig. 20) consists of 5 segments, the third of which reaches as far as the distal end of the basis of the right leg. The distal segment is small and inserted a short distance before the end of the fourth segment; the two segments together thus form a chela (figs. 21 and 22). Distally on the last segment are 2 teeth, which are curved outward. The right fifth leg consists of a well-developed, 2-segmented basipod, a 2-segmented exopod, and a 1-segmented endopod. The first exopodal segment bears 4 triangular processes along the internal margin—3 on the proximal half, and 1 near the distal end of the margin. The distal segment has a triangular process along the internal margin, at about one-third the length from the proximal end, and a row of small teeth distal to the process. The endopod is S-shaped and has 3 triangular processes along the external margin.

Euchirella unispina, new species

(Plate 6, figs. 1–21; plate 7, figs. 1–11)

Occurrence

- Sta. 3. 6 adult females, 4.28 to 4.56 mm.
- Sta. 5. 7 adult females, 4.60 to 4.70 mm.;
1 adult male, 3.84 mm.
- Sta. 7. 3 adult females, 4.70 to 4.80 mm.;
1 adult male, 3.93 mm.
- Sta. 9. 3 adult females, 4.60 to 4.89 mm.;
3 adult males, 3.93 to 4.03 mm.

Description of Female

The total length is from 4.28 to 4.89 mm. The prosome is about 4.3 times longer than the urosome. The first metasomal segment is fused with the cephalosome, but a line of demarca-

tion is often visible in stained specimens. The fourth and fifth metasomal segments are completely fused. The forehead in dorsal aspect (plate 6, fig. 1) is slightly triangular and in lateral aspect (plate 6, fig. 2) smoothly curved into a powerful rostrum. The rostrum is single, points forward, and has an acute apex. The base of the rostrum has a distinct constriction from which 2 sensory hairs arise.

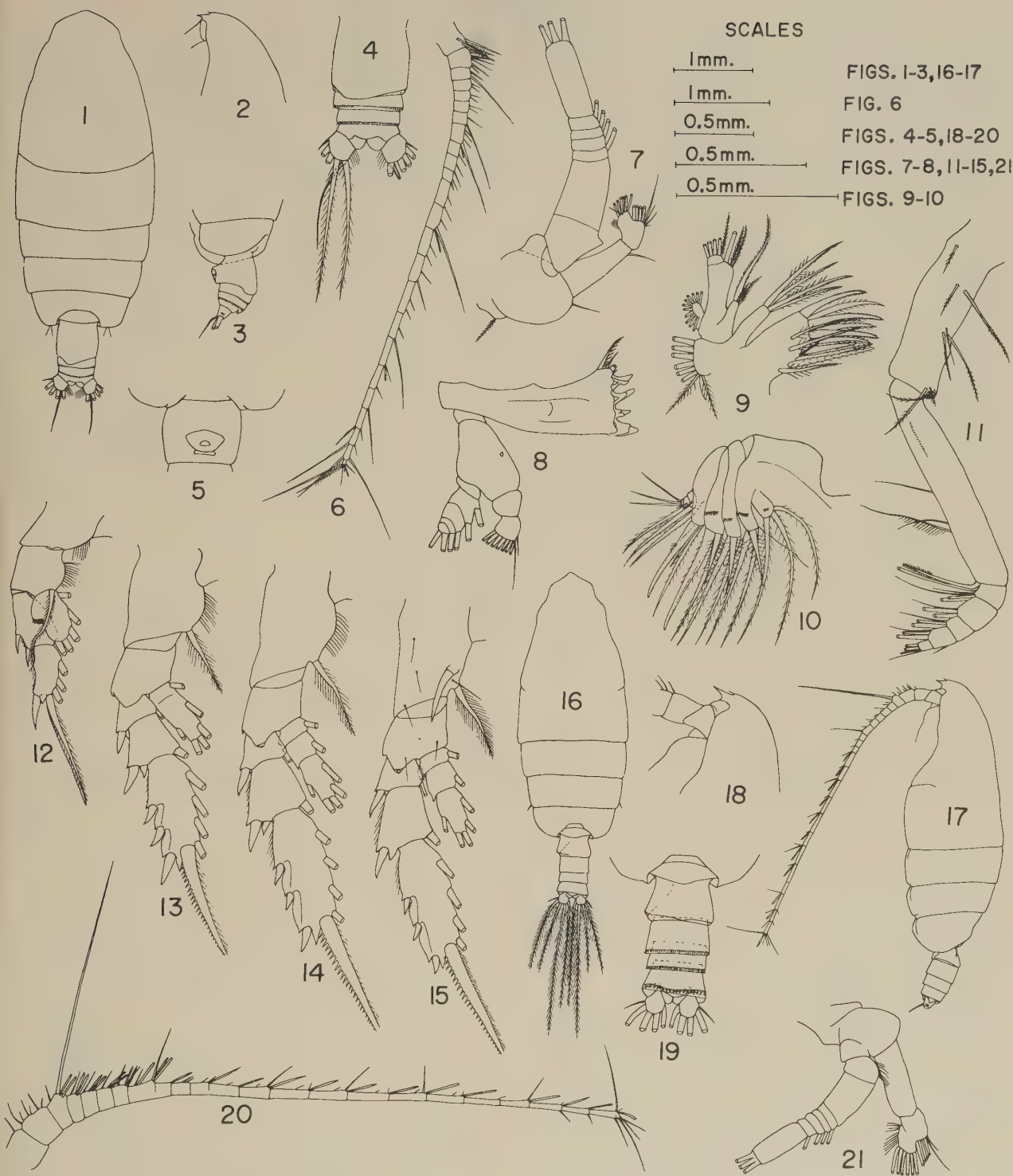
The posterolateral margins of the metasome are rounded. The urosome (plate 6, figs. 3–5) is 4-segmented; the segments and the caudal rami have the following proportional lengths, from anterior to posterior: 51:12:12:11:14. The genital segment is about as long as it is wide and slightly asymmetrical in dorsal aspect, as it is produced distally on the left side. The caudal rami are wider than long (24:19) and have 4 strong, subequal terminal setae, a short, strong external seta, and a curved internal seta.

The 24-segmented antennule reaches the end of the caudal ramus when folded back. The arrangement of the various setae and the aesthetes is illustrated in plate 6, figure 6.

The antenna (plate 6, fig. 7) has a short endopod, about equal to the first 2 exopodal segments combined. The first endopodal segment has 1 seta near the distal end of the internal margin, and the second endopodal segment has 8 setae on the internal and 6 + 1 setae on the external lobe. The exopod is 7-segmented; the proximal segment is produced into a triangular process near the distal end of the internal margin. Each of the 4 intermediate segments has 1 strong, plumose seta, and the elongate distal segment has 3 apical setae.

The cutting edge of the mandibular blade (plate 6, fig. 8) is armed with five groups of strong teeth and 2 basal spines. The posterior surface of the basis has a small process. The endopod is 2-segmented; the first segment lacks setae, but the second segment bears 9 apical setae. The exopod is 5-segmented, the segments together having 6 setae.

In the maxillule (plate 6, fig. 9), the first inner lobe is elongate, and has 12 strong spines plus 1 small spine. The second and third inner lobes are well developed; the second has 4 setae of subequal length and the third 1 large plus 2 small setae. The first outer lobe is low and has 8 setae. The basis is elongate and has 1



SCALES

1mm.

FIGS. 1-3, 16-17

1mm.

FIG. 6

0.5mm.

FIGS. 4-5, 18-20

0.5mm.

FIGS. 7-8, 11-15, 21

0.5mm.

FIGS. 9-10

PLATE 6. Figs. 1-21, *Euchirella unispina*, new species. Female: fig. 1, habitus, dorsal view; fig. 2, fore-head, lateral view; fig. 3, posterior part of metasome and urosome, lateral view; fig. 4, urosome, dorsal view; fig. 5, genital segment, ventral view; fig. 6, antennule; fig. 7, antenna; fig. 8, mandible; fig. 9,

maxillule; fig. 10, maxilla; fig. 11, maxilliped; fig. 12, first leg; fig. 13, second leg; fig. 14, third leg; fig. 15, fourth leg. Male: fig. 16, habitus, dorsal view; fig. 17, habitus, lateral view; fig. 18, fore-head, lateral view; fig. 19, posterior part of metasome and urosome, dorsal view; fig. 20, left antennule; fig. 21, antenna.

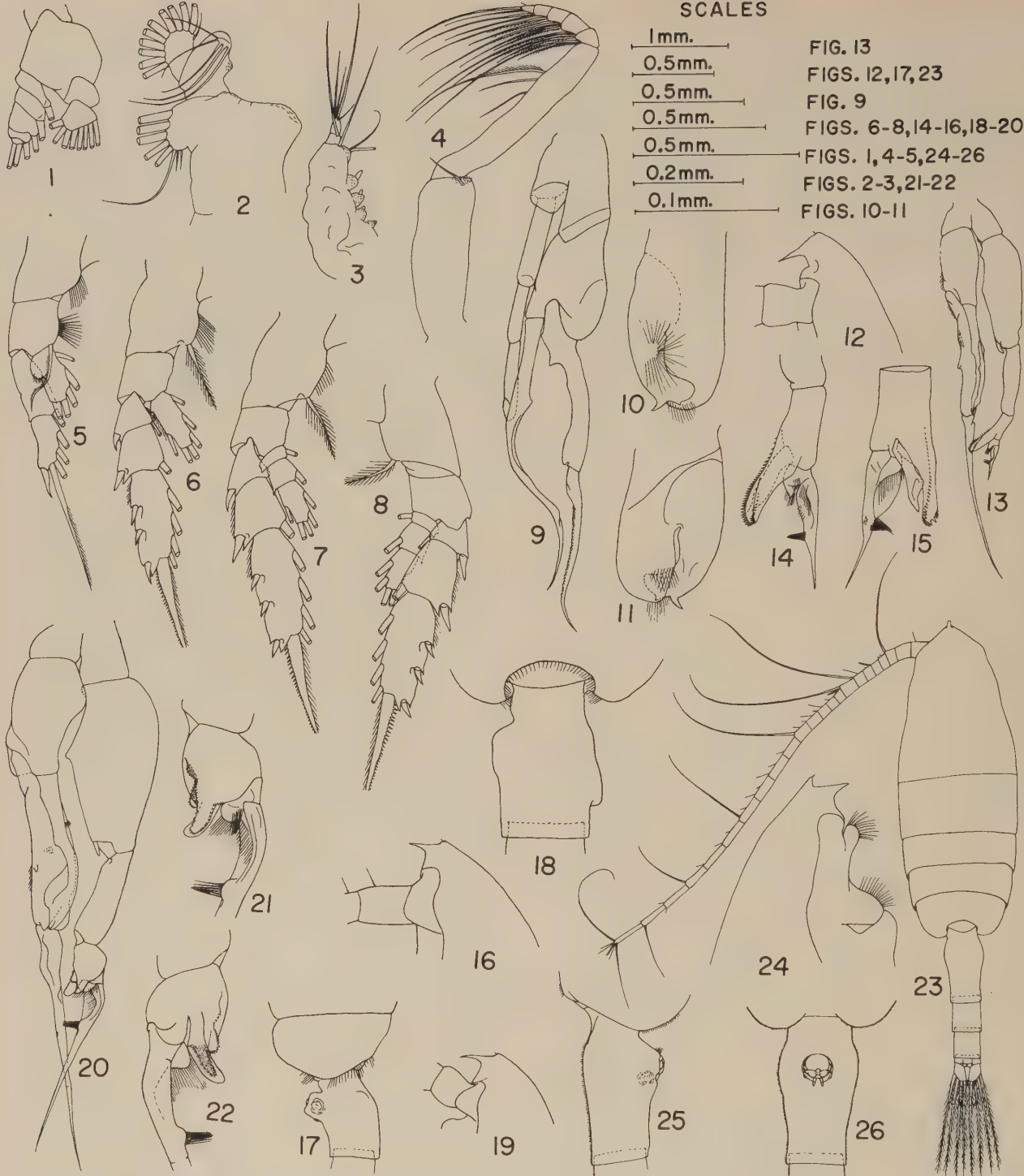


PLATE 7. Figs. 1-11, *Euchirella unispina*, new species. Male: fig. 1, mandibular palp; fig. 2, maxillule; fig. 3, maxilla; fig. 4, maxilliped; fig. 5, first leg; fig. 6, second leg; fig. 7, third leg; fig. 8, fourth leg; fig. 9, fifth pair of legs, posterior aspect; fig. 10, terminal part of left fifth leg, posterior aspect; fig. 11, *idem*, anterior aspect. Figs. 12-15, *Euchaeta spinosa*. Male: fig. 12, forehead, lateral view; fig. 13, fifth pair of legs, anterior aspect; fig. 14, distal part of left fifth leg, anterior aspect; fig. 15, *idem*, posterior aspect.

pect. Figs. 16-22, *Euchaeta media*. Female: fig. 16, forehead, lateral view; fig. 17, posterior part of metasome and genital segment, lateral view; fig. 18, *idem*, dorsal view. Male: fig. 19, forehead, lateral view; fig. 20, fifth pair of legs, anterior aspect; fig. 21, middle part of exopod of left fifth leg, anterior aspect; fig. 22, *idem*, posterior aspect. Figs. 23-26, *Euchaeta wrighti*, new species. Female: fig. 23, habitus, dorsal view; fig. 24, forehead, lateral view; fig. 25, genital segment, lateral view; fig. 26, *idem*, ventral view.

large and 2 small setae at the inner apex. The endopod and the exopod are small and 1-segmented, and have 5 and 11 setae, respectively.

The maxilla (plate 6, fig. 10) is short and has 5 prominent lobes. Each of the first to fourth lobes has a transverse row of small spinules on the posterior surface. The first lobe has in addition 3 long spinulose setae and 1 short, spinulose seta; the second and third lobes each have 2 long spinulose setae and one short spinulose seta; and each of the fourth and fifth lobes has one strong, dagger-shaped spine, 1 long spinulose seta, and 1 short spinulose seta. The endopod seems to be 4-segmented. Each of the first 3 segments has 1 spinulose seta. These setae are about equally long. The terminal segment has 3 short setae. In addition, the second and third segments each have a tiny seta.

The maxilliped (plate 6, fig. 11) has a slender basipod, and a short endopod that is about one-half the length of the basis. The coxa has four groups of setae, composed of 1, 2, 3, and 3 setae, respectively. Some scattered spinules are at the insertions of the setae of the last group. The basis has 3 setae at the middle and 2 setae at the distal end of the internal margin, in addition to a row of spinules along the proximal portion of the same margin. The endopod consists of 5 segments which have 4, 3, 3, 3 + 1, and 4 setae, respectively.

The first pair of legs (plate 6, fig. 12) has 2-segmented exopods and 1-segmented endopods. The basipod is fringed with hairs along the internal margin and has a seta at the distal end of the same margin. The endopod is slightly shorter than the first exopodal segment, and its external margin has a round tubercle that bears a transverse row of spinules on the anterior surface. The endopod has 3 internal setae and 2 apical setae. The first exopodal segment has 1 internal seta and 2 subequal external spines. The second exopodal segment has 1 strong external spine, 3 internal setae, and 1 long apical spine.

In the basipod of the second leg (plate 6, fig. 13), the coxa is fringed with hairs only along the internal margin and has an internal seta. The endopod is a single segment (a line of fusion is visible in stained specimens) that is slightly shorter than the combined length of

the first and second exopodal segments. The endopod has 3 internal setae, 1 external seta, and 2 apical setae. The first and second exopodal segments each have 1 internal seta and 1 strong external spine. The third exopodal segment is longer than the first and second segments combined and has 3 strong external spines, 4 internal setae, and 1 long terminal spine that is armed with a row of acute teeth along the external margin.

The third leg (plate 6, fig. 14) is slightly larger than the second, but its basipod and exopod are similar in anatomical details to those of the second. The endopod is 3-segmented; the segments have 1, 1, and 5 setae, respectively. There are 2 triangular, flattened processes along the external margin of the first endopodal segment.

The fourth leg (plate 6, fig. 15) is slightly smaller than the third, and its coxa has a strong spine in addition to a stout internal seta. The spine extends beyond the distal end of the segment. Furthermore, the posterior surface of the coxa has 4 delicate setae, one of which is immediately distal to the insertion of the spine. Two such setae are also on the posterior surface of the basis. The exopod and endopod are anatomically similar to those of the third leg. The fifth pair of legs is absent.

Description of Male

The total length ranges from 3.84 to 4.03 mm. The proportional length of the prosome to the urosome is about 3.7:1. The prosome is more slender than in the female and has a low triangular forehead in dorsal aspect (plate 6, fig. 16). In lateral view the forehead is smoothly rounded into a strong rostrum and devoid of crests (plate 6, fig. 18). The cephalosome and the first metasomal segment, as well as the fourth and fifth metasomal segments, are completely fused, as they are in the female. The posterolateral margins of the metasome are rounded.

The urosome (plate 6, fig. 19) consists of 5 free segments and the caudal rami. The segments and the caudal rami have the following proportional lengths, from anterior to posterior: 25:24:17:19:6:9. The distal margins of the second to fourth urosomal segments are each fringed with a row of small spinules.

The 24-segmented antennule (plate 6, figs. 17 and 20) reaches the end of the second urosomal segment when applied against the body. Articulations between the 8th and 9th, the 11th and 12th, and the 23d and 24th segments are incomplete.

In the antenna (plate 6, fig. 21), the endopod is much better developed than in the female, reaching about two-thirds the length of the exopod. The basipod and the first endopodal segment, however, are devoid of setae.

The mouth parts are all reduced. The mandible (plate 7, fig. 1) lacks the mandibular blade. In the maxillule (plate 7, fig. 2), the first inner lobe is reduced to a mere round process that lacks setae or spines, and the second and third inner lobes are absent. The basis has no setae. The endopod is small, with 5 setae, but the exopod is much better developed than in the female and has 10 large setae plus 1 small seta.

In the maxilla (plate 7, fig. 3), the first to fourth lobes lack setae or spines. The fifth lobe has 2 setae. The endopod is 2-segmented and has 1 seta on the first and 4 setae on the second segment. In addition, there is a seta at the insertion of the endopod. The coxa of the maxilliped (plate 7, fig. 4) has a single seta and some scattered spinules on the distal lobe.

The legs of the male differ from those of the female in certain respects. In the first leg (plate 7, fig. 5), the first exopodal segment lacks external spines. The endopod of the second leg (plate 7, fig. 6) is a single segment without a visible line of fusion. The fourth leg (plate 7, fig. 8) lacks coxal spines and closely resembles the third (plate 7, fig. 7), but differs from the same leg of the female.

The fifth pair of legs (plate 7, fig. 9) consists of a uniramous left leg and a well-developed, biramous right leg. The left leg has 5 segments. The small distal segment is inserted a short distance proximal to the end of the preceding segment; the 2 segments together thus form a minute chela. The distal segment carries 2 teeth apically. The external tooth, which is the larger, curves outward, the internal one inward (plate 7, figs. 10 and 11). The right leg consists of a 2-segmented basipod, a 1-segmented endopod, and a 2-segmented exopod. The basipod is well developed, reaching the middle of the third segment of the left leg.

The endopod is S-shaped, and has a triangular prominence along the external margin, one-third the length from the proximal end. The first exopodal segment has 2 prominences along the proximal one-third of the internal margin; the distal one of these is much larger than the other. The distal segment is S-shaped and has a row of small teeth along the internal margin.

Remarks

This species is closely related to *E. truncata*, but the female can easily be distinguished from that of the latter by her smaller size and the shape of the genital segment. The male of this species is characterized by the shapes of the teeth on the terminal segment of the left fifth leg and by the arrangement of the prominences on the exopod and endopod of the right fifth leg.

Type material of *E. unispina* from station 5 has been deposited in the U.S. National Museum as follows: Holotype female (USNM 113238); allotype male (USNM 113239); six females as paratypes (USNM 113240).

Euchirella amoena Giesbrecht, 1888

Occurrence

- Sta. 3. 1 adult female, 3.84 mm.;
1 adult male, 3.20 mm.;
3 fifth copepodid females, 2.89 to 3.07 mm.;
4 fifth copepodid males, 3.00 to 3.09 mm.
- Sta. 5. 2 adult females, 3.74 to 3.84 mm.;
3 adult males, 3.45 to 3.55 mm.;
2 fifth copepodid males, 3.26 mm.
- Sta. 7. 1 fifth copepodid female, 3.13 mm.;
1 fifth copepodid male, 3.16 mm.
- Sta. 9. 1 fifth copepodid female, 3.00 mm.

Remarks

The male of this species had been known as *E. amoena* and the female as *E. brevis*, until Grice (1962) synonymized them.

The female is well characterized by the stout, almost globose body, the last metasomal segment (with a pointed ridge on its posterolateral margin), and by the presence of 4 small acute teeth near the base of the internal seta of the coxa of the fourth leg.

The adult male can be recognized easily by the characteristic fifth pair of legs, which has a strong spine on the internal margin of the first segment of the right exopod. The fifth copepodid male is distinguished by the mandible, which, like that of the adult female, has a strong spine on the basis.

Euchirella rostrata Claus, 1866

Occurrence

- Sta. 5. 12 adult females, 3.26 to 3.45 mm.
Sta. 7. 22 adult females, 3.36 to 3.64 mm.;
1 adult male, 2.97 mm.
Sta. 9. 17 adult females, 3.36 to 3.74 mm.;
1 adult male, 3.00 mm.
Sta. 13. 3 adult females, 3.60 to 3.80 mm.
Sta. 15. 6 adult females, 3.80 to 4.00 mm.

Remarks

This species is one of the most common in the present collections, but the male is rare.

Undeuchaeta plumosa Lubbock, 1856

Occurrence

- Sta. 5. 4 adult females, 3.74 to 3.93 mm.
Sta. 9. 5 adult females, 3.84 to 4.12 mm.;
2 adult males, 3.55 to 3.72 mm.

Remarks

The present specimens are in full agreement with the figures given by Grice (1962).

FAMILY EUCHAETIDAE

Euchaeta marina (Prestandrea, 1833)

Occurrence

- Sta. 3. 1 fifth copepodid female, 2.90 mm.;
3 adult males, 3.60 to 3.74 mm.
Sta. 5. 1 adult female, 3.55 mm.

Remarks

According to Grice (1962), this species is fairly common in the equatorial Pacific Ocean, but it seems to be rare in the central North Pacific.

Euchaeta spinosa Giesbrecht, 1892
(Plate 7, figs. 12-15)

Occurrence

- Sta. 3. 5 adult females, 6.24 to 6.43 mm.;
1 adult male, 6.24 mm.

- Sta. 5. 13 adult females, 6.33 to 6.91 mm.;
7 adult males, 5.97 to 6.24 mm.

- Sta. 7. 3 adult females, 6.33 to 6.72 mm.;
1 adult male, 6.33 mm.

- Sta. 9. 2 adult females, 6.33 mm.;
4 adult males, 6.14 to 6.52 mm.

- Sta. 13. 3 adult females, 6.81 to 7.20 mm.

Remarks

The female of this species can easily be recognized by the high frontal prominence of the head, the slender rostrum, and the asymmetrical genital segment.

The male has a very slender body with a triangularly produced forehead (fig. 12). The right fifth leg (fig. 13) has a 2-segmented exopod and a 1-segmented endopod; the endopod is as long as the first segment of the exopod. The left fifth leg has a 3-segmented exopod and a small rudimental endopod. The second exopodal segment has distally a projection which is as long as the segment itself and which has a row of acute, triangular teeth along the margin (figs. 14 and 15).

Euchaeta media Giesbrecht, 1888
(Plate 7, figs. 16-22)

Occurrence

- Sta. 5. 2 adult females, 4.03 to 4.12 mm.
Sta. 9. 11 adult females, 4.22 to 4.51 mm.;
5 adult males, 3.79 to 4.03 mm.
Sta. 13. 1 adult female, 4.51 mm.

The female (figs. 16-18) is well characterized by the shape of the genital segment, but the description of the male is rather incomplete (Wilson, 1950). The following description was made from the specimens from station 9.

Description of Male

The total length ranges from 3.79 to 4.03 mm. The proportional lengths of the prosome and urosome are 2.2:1. The forehead in dorsal aspect is produced triangularly, but in lateral view is smoothly rounded into a slender rostrum that is curved slightly downward (fig. 19). The antennule is 23-segmented and reaches to about the distal end of the metasome.

The right fifth leg (fig. 20) consists of a stout basipod, a 2-segmented exopod, and a 1-segmented endopod. The endopod is shaped like a ladle and is equal in length to the proxi-

mal exopodal segment. The second exopodal segment is like an elongated spine, enlarged at its base and acuminate at the tip. The left fifth leg has a much stouter basipod, a 3-segmented exopod, and a rudimental endopod. Three projections arise from the mediiodistal corner of the second exopodal segment, and two of them have a row of teeth along the margin (figs. 21 and 22). The third exopodal segment is tapered distally into a slender spine; the proximal portion of the segment is hollow along the internal margin, which is fringed with long hairs; at the distal end of the hollow portion is a small knob, which has a few slender spines.

Remarks

Tanaka (1958) considered *Euchaeta acuta* var. *pacifica*, established solely on the male by Esterly (1911), synonymous with *E. media*. Esterly's description of the fifth pair of legs (the only structure described) however, seems too brief for a positive identification of the form.

Euchaeta pubera Sars, 1907

Occurrence

Sta. 5. 1 adult female, 3.84 mm.

Sta. 7. 3 adult females, 4.32 to 4.41 mm.

Remarks

The female is well characterized by the evenly rounded posterolateral corners of the metasome; the symmetrical genital segment, which in dorsal aspect is equally swollen on each side; and the hooklike process at the right side of the genital orifice. The posterior part of the body is covered with fine hairs.

Euchaeta wrighti, new species

(Plate 7, figs. 23-26; plate 8, figs. 1-3)

Occurrence

Sta. 3. 1 adult female, 2.73 mm.

Description of Female

The proportional lengths of the prosome and urosome are about 2:1. The general shape of the body is slender (plate 7, fig. 23). The cephalosome and the first metasomal segment, as well as the fourth and fifth metasomal segments, are fused, but a line of fusion between

the cephalosome and the first metasomal segment is clearly visible after staining. The forehead in both dorsal and lateral view is produced into a process, which carries a sensory hair (plate 7, fig. 24). The rostrum is strong, pointing straight downward. The posterolateral margins of the metasome are smoothly rounded.

The urosome is 4-segmented; the segments, with the caudal rami, have the following proportional lengths, from anterior to posterior: 44:22:17:6:11.

The genital segment (plate 7, figs. 25 and 26) is long and slender. In dorsal aspect it is almost perfectly symmetrical—equally swollen on both sides. At about one-third the length from the proximal end it has a large genital swelling, clearly visible in lateral aspect. The distal portion of the metasome and the whole urosome are densely covered with very fine hairs.

The antennule is 23-segmented, and, when fully extended, reaches as far as the end of the caudal ramus. The maxillule is best described by reference to plate 8, figure 1. In the maxilla, one of the 6 apical setae has long spines, in addition to short spinules that cover it entirely.

The basipod of the first leg (plate 8, fig. 2) is fringed with hairs along the internal margin and has the customary curved seta on the distal medial end of the basis. The exopod is 2-segmented. The external margin of the first segment is almost straight and has a fine spine near the distal end; the internal margin has a single seta. The second segment has a fine external spine, 3 internal setae, and 1 terminal spine, which is about four times as long as the segment. The endopod is a single segment; its external margin has a round tubercle armed with a row of fine spinules, the internal margin has 3 setae, and the apex 2 setae.

The coxa of the second leg (plate 8, fig. 3) has a row of hairs and a strong seta on the internal margin. The exopod is 3-segmented, with relatively small external spines. Of these spines the one on the second segment is the largest, but it does not reach as far as the base of the first external spine of the third segment. The terminal spine of the exopod is about as long as the third exopodal segment. The endopod is a single segment and is slightly shorter than the first 2 exopodal segments combined.

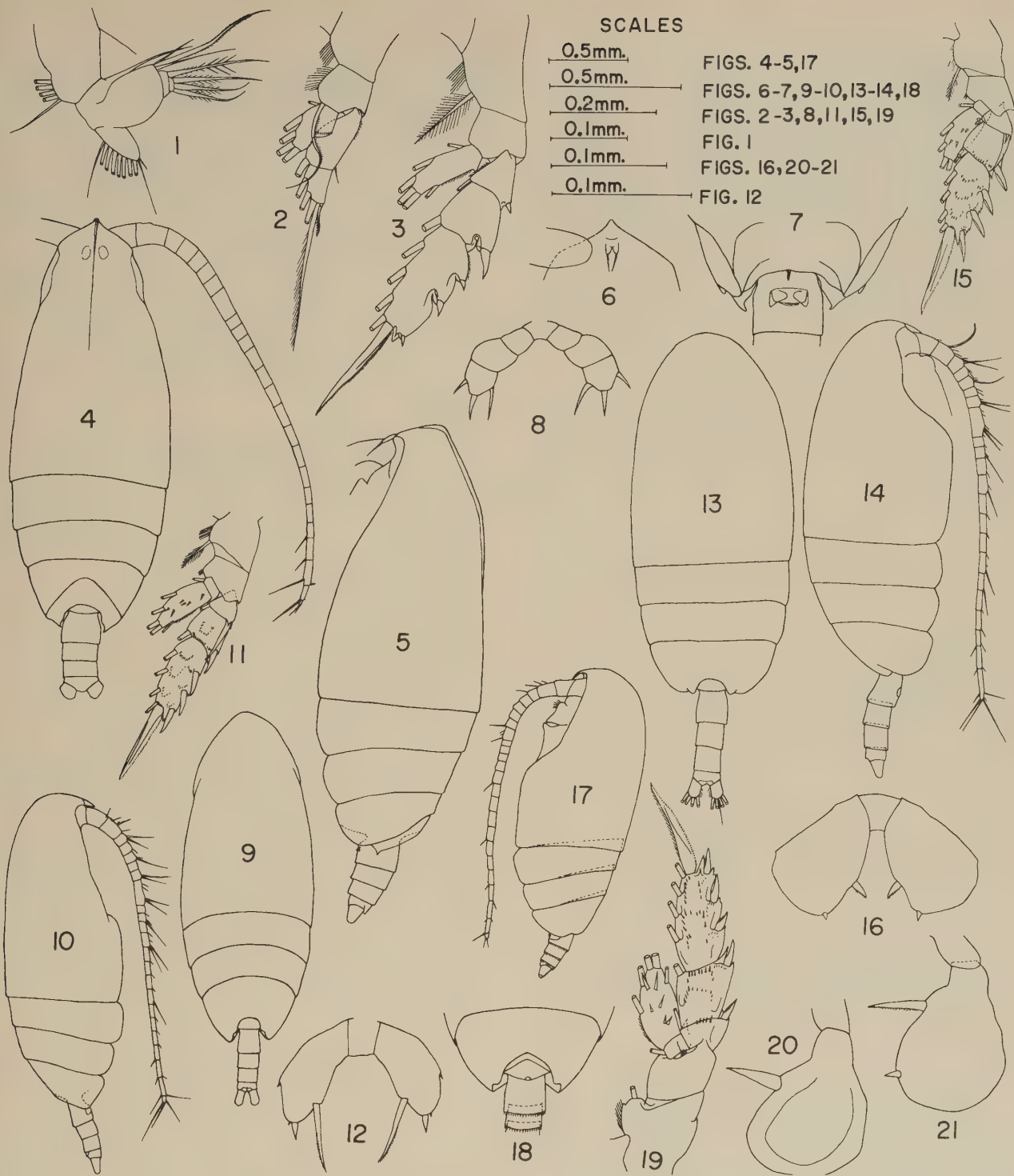


PLATE 8, Figs. 1-3, *Euchaeta wrighti*, new species. Female: fig. 1, maxillule; fig. 2, first leg; fig. 3, second leg. Figs. 4-8, *Lophothrix latipes*. Female: fig. 4, habitus, dorsal view; fig. 5, habitus, lateral view; fig. 6, forehead, ventral view; fig. 7, posterior part of metasome and genital segment, ventral view; fig. 8, fifth pair of legs. Figs. 9-12, *Scolecithricella minor*. Female: fig. 9, habitus, dorsal view; fig. 10, habitus, lateral view; fig. 11, second leg; fig. 12, fifth pair of

legs. Figs. 13-16, *Scolecithricella dentata*. Female: fig. 13, habitus, dorsal view; fig. 14, habitus, lateral view; fig. 15, second leg; fig. 16, fifth pair of legs. Figs. 17-21, *Scolecithricella ovata*. Female: fig. 17, habitus, lateral view; fig. 18, posterior part of metasome and anterior part of urosome, dorsal view; fig. 19, second leg; fig. 20, left fifth leg; fig. 21, right fifth leg.

Remarks

Although only a single specimen was found, I believe that its characters are sufficiently distinct to consider it as a member of a valid species. The present specimen, in general shape of the body, appears to be related to *E. plana* Mori, 1937, redescribed by Tanaka (1958). The obvious difference in the location of the genital swelling, however, prevents it from being referred to that species.

The only specimen was accidentally destroyed.

FAMILY PHAENNIDAE

Phaenna spinifera Claus, 1863

Occurrence

Sta. 3. 10 adult females, 1.84 to 2.11 mm.;
1 adult male, 1.94 mm.

Sta. 5. 5 adult females, 1.91 to 2.40 mm.

Sta. 7. 5 adult females, 2.02 to 2.11 mm.

Remarks

This species can readily be recognized by the nearly rounded body in dorsal aspect. In details the present specimens are in full agreement with the figures given by Giesbrecht (1892).

FAMILY SCOLECITHRICIDAE

Lophothrix latipes (T. Scott, 1894) (Plate 8, figs. 4-8)

Occurrence

Sta. 3. 1 adult female, 3.06 mm.

Sta. 5. 9 adult females, 3.03 to 3.16 mm.

Sta. 7. 1 adult female, 3.23 mm.

Remarks

This species can be recognized by the following characters: The head has a long, low crest and two large ocular lenticels that are clearly visible in stained specimens (figs. 4 and 5). The rostrum consists of a thickened, incised basal portion, which has two fine rostral filaments (fig. 6). The posterolateral corner of the metasome (fig. 7) is produced into a point, the tip of which in dorsal or ventral view curves inward and reaches to about the middle of the genital segment. The fifth leg (fig. 8) is uniramous and 4-segmented; it is considerably

dilated toward the distal end and has 3 spines on the apex. The inner spine is the longest.

Scolecithrix danae (Lubbock, 1856)

Occurrence

Sta. 3. 3 fifth copepodid females, 1.50 to 1.55 mm.;

2 adult males, 2.07 to 2.10 mm.

Sta. 5. 8 adult females, 2.01 to 2.17 mm.;

6 adult males, 2.11 to 2.17 mm.

Sta. 7. 4 adult females, 2.14 to 2.17 mm.;

1 adult male, 2.11 mm.

Remarks

The female of this species can readily be distinguished by her very robust body and by the genital segment, which has a ventral projection in the form of a shovel. Giesbrecht (1892) and Rose (1942) have described and figured this species in detail.

Scolecithrix bradyi Giesbrecht, 1888

Occurrence

Sta. 3. 1 adult female, 1.22 mm.

Sta. 5. 2 adult females, 1.32 mm.;

1 adult male, 1.51 mm.

Sta. 7. 5 adult females, 1.32 to 1.38 mm.

Sta. 9. 1 adult female, 1.40 mm.

Remarks

The asymmetrical last metasomal segment and the extremely short urosome identify the female of this species and the structure of the fifth pair of legs identifies the male. Figures of these characters have been given by Grice (1962).

Scolecithricella minor (Brady, 1883) (Plate 8, figs. 9-12)

Occurrence

Sta. 16. 1 adult female, 1.42 mm.

Remarks

The urosome of the female has a characteristic shape; it is markedly narrow as compared with its robust prosome (figs. 9 and 10). The posterolateral margin of the metasome in lateral view is triangularly produced into a blunt tip, which reaches the middle of the genital segment. The first exopodal segment of the sec-

ond leg (fig. 11) has a long external spine that extends beyond the distal margin of the second exopodal segment. The fifth leg (fig. 12) consists of a basal portion, common to both legs, and a plate-shaped apical segment, which has a long internal spine, a short, strong apical spine, and a small external spine. An additional small spine is located immediately lateral to the apical spine.

Scolecithricella dentata (Giesbrecht, 1892)
(Plate 8, figs. 13–16)

Occurrence

- Sta. 5. 1 adult female, 1.48 mm.
Sta. 15. 1 adult female, 1.55 mm.
Sta. 16. 1 adult female, 1.68 mm.

Remarks

The following characters mainly serve to identify the female of this species: The prosome is nearly elliptical in dorsal aspect (fig. 13); its posterolateral margin in lateral aspect (fig. 14) has a distinct incision that is also clearly visible in dorsal view. The external spine of the first exopodal segment of the second leg (fig. 15) is long, slightly curved inward, and reaches the distal margin of the second exopodal segment. On the third exopodal segment of the same leg, 3 small teeth lie along the external margin immediately proximal to each of the second and third external spines. The fifth leg (fig. 16) is laminate and almost rectangular; it has a tiny spine at the tip and a larger spine on the internal margin.

Scolecithricella ovata (Farran, 1905)
(Plate 8, figs. 17–21)

Occurrence

- Sta. 5. 1 adult female, 1.98 mm.
Sta. 7. 1 adult female, 1.88 mm.

Remarks

The female of this species can easily be distinguished by the posterolateral margin of the metasome, which has a distinct notch visible in either lateral or dorsal view (figs. 17 and 18), and by the second and fifth pairs of legs. The coxa of the second leg (fig. 19) has a distinct notch on the external margin; the roundly produced internal margin also has a distinct notch, in addition to a row of hairs and a seta.

The fifth leg (fig. 20) is shaped like a paddle with a cylindrical "handle" by which it is attached to a common basal portion. The internal margin of the paddle-shaped portion has a well-developed spine. One specimen had a small second internal spine close to the distal end of the right leg (fig. 21).

Scolecithricella vittata (Giesbrecht, 1892)

Occurrence

- Sta. 5. 2 adult females, 1.74 to 1.80 mm.

Remarks

The female is readily recognized by the characteristic fifth pair of legs. Figures of this and other characters have been given by Grice (1962).

Scolecithricella auropecten (Giesbrecht, 1892)
(Plate 9, figs. 1–4)

Occurrence

- Sta. 5. 9 adult females, 2.17 to 2.37 mm.
Sta. 7. 6 adult females, 2.11 to 2.34 mm.
Sta. 13. 1 adult female, 2.40 mm.

Remarks

The female of this species can be identified easily by the posterolateral margin of the metasome, which in lateral view has a round depression (fig. 1), and by the fifth pair of legs (fig. 2). Figures of the mouth parts and the swimming legs have been given by Rose (1942) and Giesbrecht (1892).

Two specimens possessed abnormal fifth pairs of legs (figs. 3 and 4) but appeared to be identical with the normal specimens in all other details.

FAMILY METRIDIIDAE

Metridia lucens Boeck, 1865

Occurrence

- Sta. 16. 2 adult females, 2.68 to 2.78 mm.;
9 fifth copepodid females, 1.90 to 2.07 mm.;
4 fifth copepodid males, 1.73 to 1.84 mm.

Remarks

This species is easily recognized by two characters. The posterolateral margin of the met-

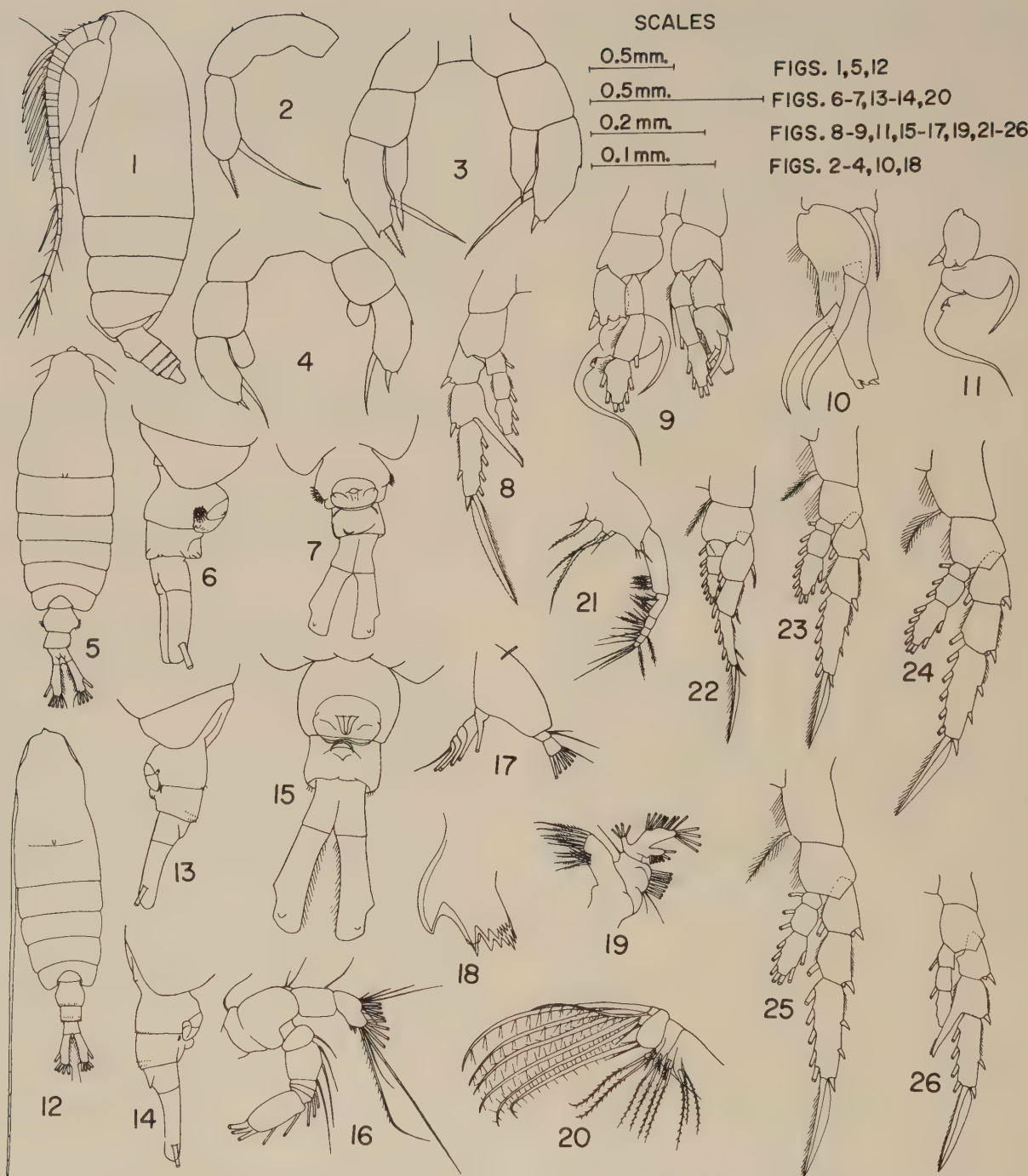


PLATE 9. Figs. 1-4, *Scolecithricella auropecten*. Female: fig. 1, habitus, lateral view; fig. 2, fifth leg; figs. 3-4, abnormal fifth pairs of legs. Figs. 5-11, *Centropages violaceus*. Female: fig. 5, habitus, dorsal view; fig. 6, posterior part of metasome and urosome, lateral view; fig. 7, *idem*, ventral view; fig. 8, fifth leg. Male: fig. 9, fifth pair of legs, anterior aspect; fig. 10, distal part of exopod of left fifth leg; fig. 11, exopod of right fifth leg. Figs. 12-26, *Centropages*

elegans. Female: fig. 12, habitus, dorsal view; fig. 13, posterior part of metasome and urosome, viewed from left side; fig. 14, *idem*, viewed from right side; fig. 15, *idem*, ventral view; fig. 16, antenna; fig. 17, mandibular palp; fig. 18, cutting edge of manducatory plate; fig. 19, maxillule; fig. 20, maxilla; fig. 21, maxilliped; fig. 22, first leg; fig. 23, second leg; fig. 24, third leg; fig. 25, fourth leg; fig. 26, fifth leg.

asome is produced into a point. In the second leg, the basis has a hook on the distal margin and the internal margin of the first endopodal segment is proximally provided with a deep invagination guarded by 3 strong teeth.

Brodsky (1950) distinguished the Pacific form of *Metridia lucens* from the Atlantic form and gave it a new name, *Metridia pacifica*. Damkaer (1964 and personal communication) examined specimens from both the Pacific and the Atlantic and found no morphological differences to warrant two species.

FAMILY CENTROPAGIDAE

Centropages bradyi Wheeler, 1900

Occurrence

- Sta. 5. 1 adult female, 1.95 mm.
Sta. 9. 1 adult male, 1.74 mm.
Sta. 13. 30 adult females, 1.91 to 2.08 mm.;
8 adult males, 1.78 to 1.91 mm.
Sta. 15. 11 adult females, 2.00 to 2.24 mm.;
2 adult males, 1.97 to 2.00 mm.

Remarks

This species is characterized by the rounded posterolateral corners of the metasome, the symmetrical genital segment, and the large caudal rami, each of which has a fingerlike projection between the two lateral terminal setae.

Centropages elongatus Giesbrecht, 1896

Occurrence

- Sta. 3. 7 adult females, 1.74 to 1.90 mm.;
7 adult males, 1.65 to 1.80 mm.
Sta. 5. 1 adult female, 1.91 mm.
Sta. 7. 1 adult female, 1.91 mm.;
1 adult male, 1.81 mm.

Remarks

The present specimens are in agreement with the figures given by Grice (1962).

Centropages violaceus (Claus, 1863) (Plate 9, figs. 5–11)

Occurrence

- Sta. 3. 1 adult female, 2.17 mm.;
4 adult males, 2.04 to 2.11 mm.
Sta. 5. 3 adult females, 2.11 to 2.14 mm.;
4 adult males, 2.04 to 2.17 mm.

- Sta. 7. 11 adult females, 2.14 to 2.24 mm.;
2 adult males, 2.14 to 2.17 mm.

Remarks

The female of this species can be distinguished by the genital segment, which in dorsal aspect (fig. 5) is slightly asymmetrical—the right side is slightly more swollen. The swellings of both the right and left sides have a group of spinules (figs. 6 and 7). The second urosomal segment ventrally lacks the knoblike projection shown in the figure by Giesbrecht (1892). In the fifth leg (fig. 8) the spiniform projection of the second exopodal segment is slightly shorter than the third exopodal segment and has a row of stiff hairs along the internal distal margin.

The male of this species can be identified by the fifth pair of legs (figs. 9–11). The second exopodal segment of the right leg is nearly elliptical; the spinous projection of the segment bends sharply outward. The terminal claw has a deep notch at the proximal portion of the internal margin; in this notch is an acute tooth.

Centropages elegans Giesbrecht, 1895 (Plate 9, figs. 12–26; plate 10, figs. 1–6)

Centropages elegans Giesbrecht, 1895, p. 256,
plate 4, figs. 1–2.

Occurrence

- Sta. 3. 21 adult females, 1.86 to 2.04 mm.;
10 adult males, 1.84 to 1.97 mm.
Sta. 5. 16 adult females, 1.94 to 2.14 mm.;
9 adult males, 1.84 to 2.01 mm.
Sta. 7. 3 adult females, 2.01 to 2.07 mm.;
4 adult males, 1.94 to 2.04 mm.

Description of Female

The total length of the specimens ranges from 1.86 to 2.14 mm. The prosome is about three times as long as the urosome. The cephalosome in dorsal aspect has a small semicircular projection at the tip and a knoblike process at the posterodorsal margin (plate 9, fig. 12). The first metasomal segment is incompletely separated from the cephalosome—a line of joint is visible only on the dorsal region. The posterolateral margins of the metasome are smoothly rounded.

The urosome (plate 9, figs. 13–15) is 3-segmented; the segments and the caudal rami have

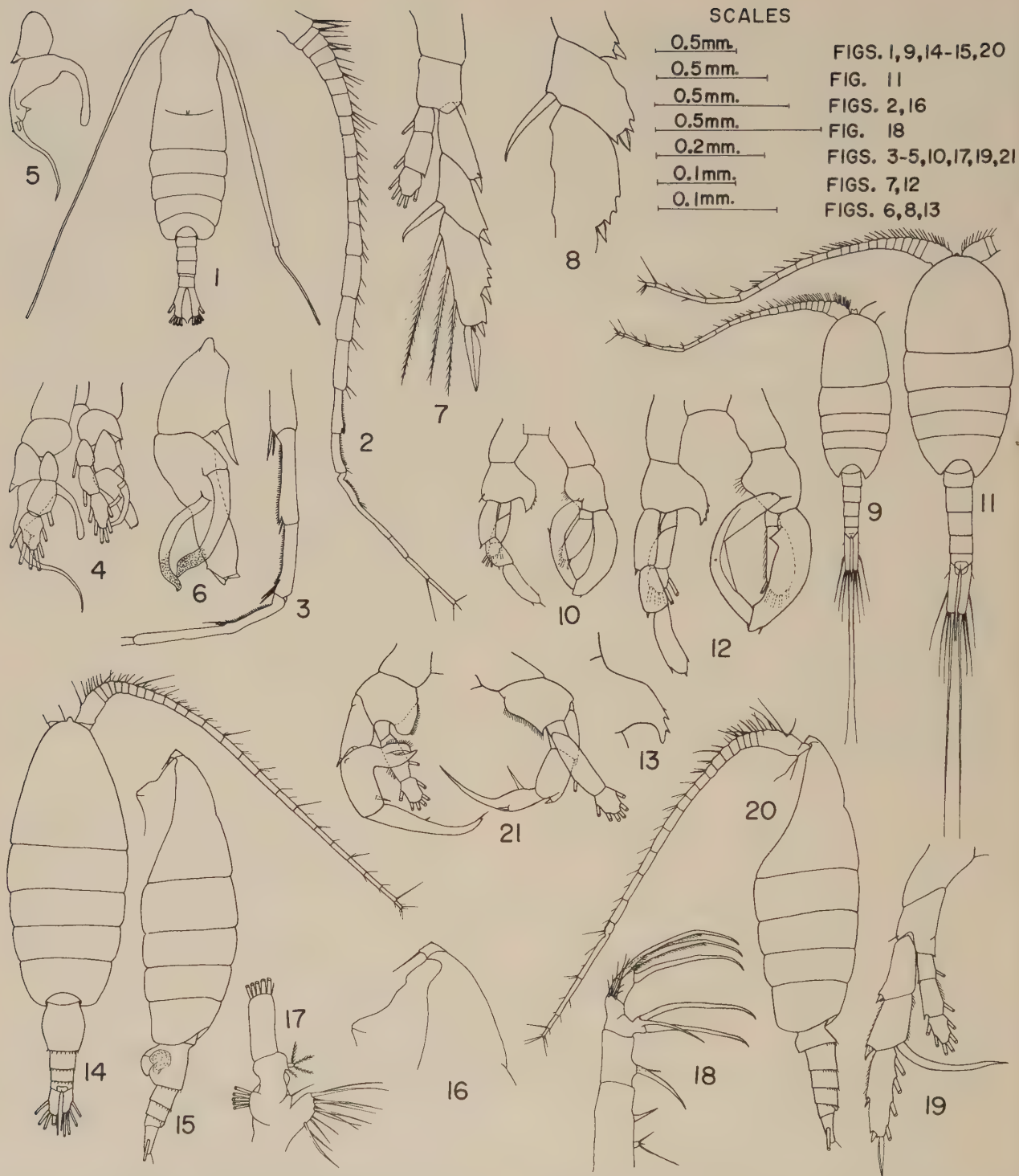


PLATE 10. Figs. 1-6, *Centropages elegans*. Male: fig. 1, habitus, dorsal view; fig. 2, right antennule; fig. 3, geniculated region of right antennule; fig. 4, fifth pair of legs, anterior aspect; fig. 5, exopod of right fifth leg; fig. 6, exopod of left fifth leg. Figs. 7-13, *Lucicutia flavicornis*. Female: fig. 7, fifth leg; fig. 8, abnormal exopod of left fifth leg. Male: fig. 9, habitus, dorsal view; fig. 10, fifth pair of legs, posterior aspect. Figs. 11-13, male abnormal in fifth pair of legs: fig.

11, habitus, dorsal view; fig. 12, fifth pair of legs, posterior aspect; fig. 13, inner projection of basis of left fifth leg. Figs. 14-21, *Heterorhabdus papilliger*. Female: fig. 14, habitus, dorsal view; fig. 15, habitus, lateral view; fig. 16, forehead, lateral view; fig. 17, maxillule; fig. 18, maxilla; fig. 19, fifth leg. Male: fig. 20, habitus, lateral view; fig. 21, fifth pair of legs, anterior aspect.

the following proportional lengths, from anterior to posterior: 28:20:16:36.

The genital segment is symmetrical, wider than long, and has dorsally a row of small spinules along its distal margin. The second urosomal segment has ventrally a knoblike projection and dorsally 2 rows of small spinules along the distal border. The caudal rami are symmetrical and about 3.5 times as long as wide.

The antennule is 24-segmented; the last 5 segments extend beyond the end of the caudal ramus. The endopod of the antenna (plate 9, fig. 16) is short—about one-half the length of the exopod. The second endopodal segment has 8 + 1 setae on the internal lobe and 6 + 1 setae on the external lobe.

The mandibular palp (plate 9, fig. 17) has a triangular basis, which has a seta on the posterior surface. The exopod is 5-segmented; each of the first to fourth segments has 1 seta, and the terminal segment 2 setae. The endopod is small; the first segment has 2 setae, and the second segment 7 setae. The mandibular blade (plate 9, fig. 18) consists of a large separate tooth and a plate with about 7 acute teeth.

The maxillule is relatively small; details of its structure are shown in plate 9, figure 19.

The maxilla (plate 9, fig. 20) is well developed. The first to fourth lobes each bear 2 + 1 spinose setae. The fifth lobe is much better developed; it has 1 long spinose seta and 2 small spiniform setae. The endopod has 5 long spinose setae, 1 short spinose seta, and a small spiniform seta.

The coxa of the maxilliped (plate 9, fig. 21) is stout and has 3 well-developed lobes. The first lobe has 1 spinose seta plus 1 spiniform seta, the second lobe 2 spinose setae plus 1 spiniform seta, and the third lobe 3 small spiniform setae. The basis is about as long as the coxa and carries 3 setae distally. The endopod is also as long as the coxa and is 5-segmented.

The basipod of the first leg (plate 9, fig. 22) is stout and has an internal seta on each segment. The endopod is 3-segmented and shorter than the first and second exopodal segments combined. The first segment has 1 internal seta; the second segment, 2 internal setae; and the third segment, 3 internal setae, 1 external seta, and 2 terminal setae. The exopod is also 3-

segmented; it has 1 + 1 + 2 external spines, 1 + 1 + 4 internal setae, and 1 terminal spine.

The second and third pairs of legs (plate 9, figs. 23 and 24) are similar. On the basipod, only the coxa has an internal seta. The endopod is 3-segmented and extends slightly beyond the distal border of the second exopodal segment. The segments have 1, 2, and 8 setae, respectively. The exopod is also 3-segmented; the first and second segments each have 1 external spine and 1 internal seta. The third segment has 3 external spines, 5 internal setae, and 1 terminal spine.

The fourth leg (plate 9, fig. 25) differs from the third leg only in the number of setae on the third endopodal segment—it has 7 setae instead of 8.

The basipod of the fifth leg has no setae (plate 9, fig. 26). The exopod is 3-segmented. The first segment has 1 external spine and a round projection along the internal margin. The second segment has 1 external spine and a strong spiniform projection from the internal margin. This projection is shorter than the third exopodal segment and has distally a row of stiff hairs along the internal margin. The third exopodal segment has 2 external spines, 4 internal setae, and a terminal spine. The endopod is also 3-segmented; it has 1 seta on the first segment, 1 on the second, and 6 on the third.

Description of Male

The total length ranges from 1.84 to 2.04 mm. The proportional lengths of the prosome and urosome are 2.8:1. The first metasomal segment is incompletely separated from the cephalosome; a line of separation is visible only on the dorsal side. The posterolateral corners of the metasome are smoothly rounded (plate 10, fig. 1). The urosome is 5-segmented; the segments and the caudal rami have the following proportional lengths, from anterior to posterior: 15:17:17:5:14:32. The caudal rami are about 3 times as long as wide.

The left antennule is 24-segmented; the last 2 segments extend beyond the end of the caudal ramus. The right antennule (plate 10, figs. 2 and 3) is modified for grasping the female. The external margins of the 17th to 19th segments are each fringed with a row of acute teeth.

The 18th and 19th segments are articulated by a "knee joint."

The antenna, the mouth parts, and the first to fourth pairs of legs are similar to those of the female.

The fifth pair of legs (plate 10, figs. 4-6) is asymmetrical—the right exopod is modified into a grasping organ in the form of a powerful chela. The left exopod is 2-segmented; the distal segment has two strong, curved spines, the distal parts of which are densely pitted.

Remarks

This species was established by Giesbrecht (1895) upon a single male specimen from the northeastern Pacific. As the species does not appear in any other lists, the present specimens constitute the first record since the original discovery. The female is described here for the first time. Sixteen female specimens have been deposited in the U.S. National Museum (USNM 113375, 113376).

FAMILY LUCICUTHIDAE

Lucicutia flavicornis (Claus, 1863)
(Plate 10, figs. 7-13)

Occurrence

- Sta. 3. 2 adult females, 1.41 to 1.43 mm.
Sta. 5. 12 adult females, 1.38 to 1.94 mm.;
6 adult males, 1.45 to 1.48 mm.
Sta. 7. 1 adult male, 1.51 mm.
Sta. 15. 3 adult females, 1.65 to 1.94 mm.
Sta. 16. 1 adult female, 2.04 mm.
1 adult male, 1.66 mm.

Remarks

The female of this species can be distinguished by the elliptical prosome and the shape of the fifth pair of legs (fig. 7). The female from station 16 had an abnormal left fifth leg—2 teeth were present proximal to the external spine of the second exopodal segment (fig. 8).

The body of the male (fig. 9) is shaped like that of the female. The left antennule is 21-segmented and slightly modified for grasping the female. The basis of the left fifth leg (fig. 10) has internally a large projection pointed distally. The internal edge of this projection has 5 or 6 teeth. In the right fifth leg, both the exopod and the endopod are 2-segmented.

The proximal exopodal segment is slightly curved inward and lacks processes on the internal margin.

Four male specimens abnormal in the shape of the fifth pair of legs were from stations 5 and 7. The general shape of the body of these males (fig. 11) does not differ from that of the normal male, but the fifth pair of legs (figs. 12 and 13) differs in the following aspects: The projection on the internal margin of the basis in the left leg is tapered distally, with 3 to 4 acute teeth along the internal edge. The first exopodal segment of the right leg has proximally a triangular process along the internal margin. The second exopodal segment of the same leg is pronouncedly curved.

FAMILY HETERORHABDIDAE

Heterorhabdus papilliger (Claus, 1863)
(Plate 10, figs. 14-21)

Occurrence

- Sta. 5. 15 adult females, 1.88 to 2.24 mm.;
14 adult males, 1.98 to 2.07 mm.
Sta. 7. 15 adult females, 1.91 to 2.31 mm.;
6 adult males, 1.94 to 2.14 mm.
Sta. 9. 4 adult females, 2.17 to 2.21 mm.;
2 adult males, 2.14 to 2.17 mm.
Sta. 13. 4 adult females, 2.41 to 2.54 mm.;
12 adult males, 2.27 to 2.65 mm.
Sta. 15. 11 adult females, 2.40 to 2.62 mm.;
4 adult males, 2.55 to 2.62 mm.
Sta. 16. 18 adult females, 2.48 to 2.58 mm.;
10 adult males, 2.48 to 2.55 mm.

Remarks

This species is one of the most common in the present collections. It can be identified readily by the triangularly produced forehead in lateral aspect (figs. 16 and 20) and the 3 equal terminal spines of the maxilla (fig. 18). In the fifth leg of the female (fig. 19), the second exopodal segment has internally a long, curved spine, which is longer than the third exopodal segment. The fifth pair of legs (fig. 21) of the male has a beaklike projection on the internal margin of the second right exopodal segment.

Heterorhabdus abyssalis (Giesbrecht, 1889)
(Plate 11, figs. 1-6)

Occurrence

Sta. 9. 3 adult females, 2.47 to 2.69 mm.;
1 adult male, 2.41 mm.

Remarks

This species is recognized by the rounded forehead in lateral aspect (fig. 2) and the structure of the maxilla (fig. 4), the distal lobe of which has 2 spines of equal length and 1 slightly shorter spine. In the fifth pair of legs of the female (fig. 3), the internal spine of the second exopodal segment is about as long as the third exopodal segment and is fringed with fine hairs along the upper margin. The fifth pair of legs in the male (figs. 5 and 6) is characterized by the laminar protrusion on the internal margin of the right basis and the conical internal projection of the second segment of the right exopod.

Heterostylites longicornis (Giesbrecht, 1889)

Occurrence

Sta. 5. 2 adult females, 2.80 to 2.83 mm.;
1 adult male, 2.90 mm.
Sta. 7. 1 adult female, 2.90 mm.

Remarks

This species is closely similar to the species of *Heterorhabdus* but can easily be distinguished from the latter by the longer antennule, the armament of the mandibular blade, and the better developed endopod of the maxilla. In the female, the second exopodal segment of the fifth leg has a compound spine, with 6 to 7 points, medial to the regular external spine.

H. longicornis is distinguished from *H. major* only by its smaller size; there are practically no anatomical differences. The female of *H. longicornis*, according to Giesbrecht and Schmeil (1898), measures about 3.0 mm., but that of *H. major* measures about 5.0 mm.

FAMILY AUGAPTILIDAE

Haloptilus longicornis (Claus, 1863)

Occurrence

Sta. 3. 136 adult females, 2.00 to 2.24 mm.
Sta. 5. 44 adult females, 2.17 to 2.44 mm.

Sta. 7. 3 adult females, 2.14 to 2.34 mm.

Remarks

This species was one of the most common at the southern stations, but not a single male was found. The female can be recognized by the knoblike projection on the forehead, when viewed from above, and the very long antennule.

Haloptilus fertilis (Giesbrecht, 1892)
(Plate 11, figs. 7-20)

Occurrence

Sta. 3. 2 adult males, 2.89 to 3.16 mm.
Sta. 5. 3 adult males, 2.93 to 3.13 mm.

This species was erected on the basis of a male from the Mediterranean Sea (Giesbrecht, 1892). Grice (1962) obtained a single male from equatorial waters of the Pacific. The following description is based on the five adult males in the present collections.

Description of Males

The total length ranges from 2.89 to 3.16 mm. The proportional lengths of the prosome and urosome are about 5.6:1. The first metasomal segment is separated from the cephalosome, but the fourth and fifth metasomal segments are fused. The cephalosome in dorsal aspect has a broadly triangular forehead, and the oral region is more or less dilated. The posterolateral margins of the metasome are smoothly rounded (fig. 7).

The urosome (fig. 8) is 5-segmented. The first segment is nearly as long as the combined lengths of the succeeding 3 segments. The figure by Giesbrecht (1892, plate 42, fig. 5), however, shows the second to fourth urosomal segments relatively longer than those of the present specimens.

The right antennule is normal, 25-segmented, and reaches as far as the end of the caudal ramus. The 23-segmented left antennule (fig. 9) is modified for grasping the female. Each of the 14th to 16th segments has a swollen outer margin, and each of the 17th to 19th segments has a serrated lamella along the same margin. A knee joint is found between the 18th and 19th segments.

In the antenna (fig. 10), the exopod is only about one-third the length of the endopod. The

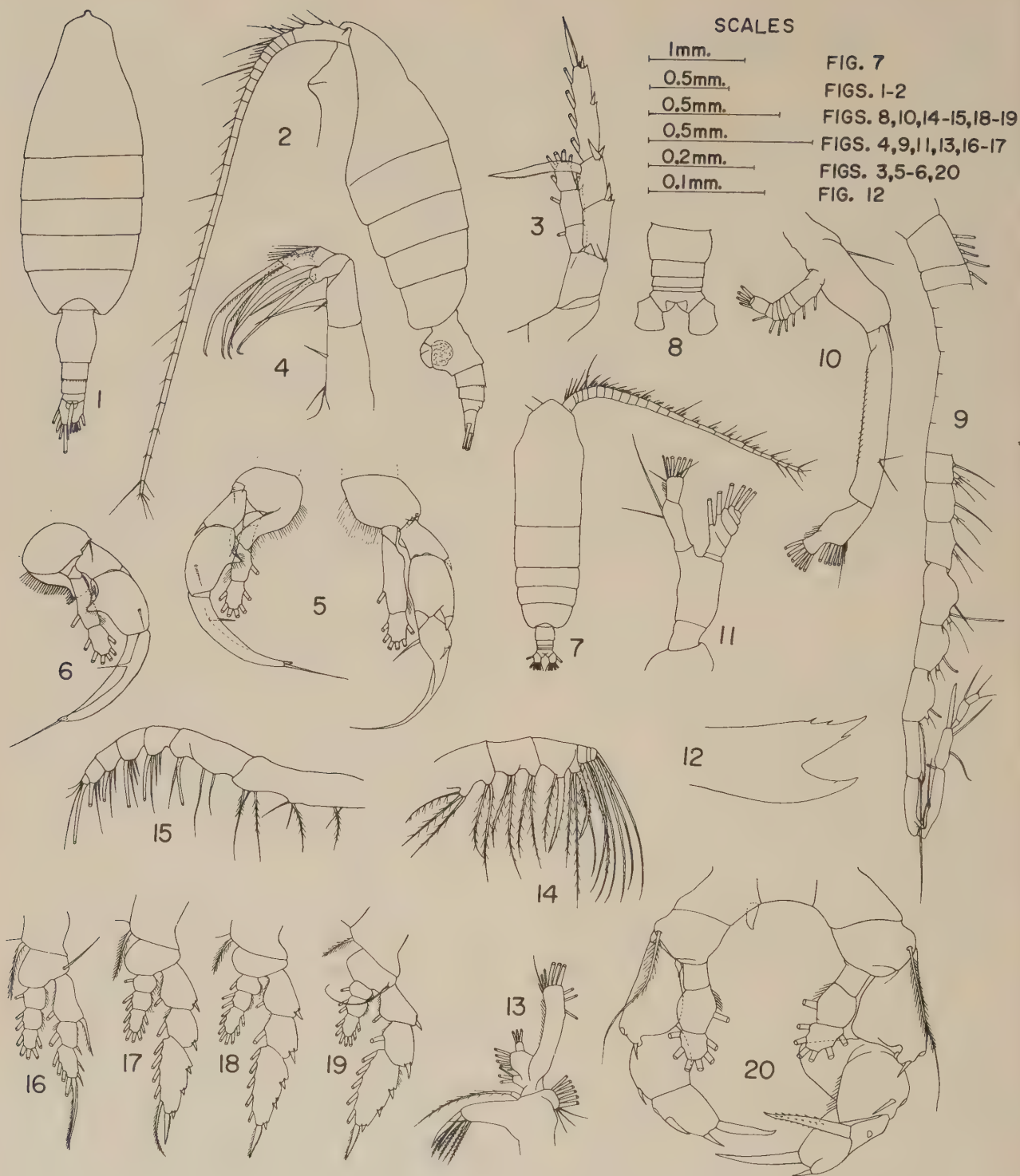


PLATE 11. Figs. 1-6, *Heterorhabdus abyssalis*. Female: fig. 1, habitus, dorsal view; fig. 2, habitus, lateral view; fig. 3, fifth leg. Male: fig. 4, maxilla; fig. 5, fifth pair of legs, anterior aspect; fig. 6, right fifth leg, posterior aspect. Figs. 7-20, *Haloptilus fertilis*. Male: fig. 7, habitus, dorsal view; fig. 8, uro-

some, dorsal view; fig. 9, left antennule; fig. 10, antenna; fig. 11, mandibular palp; fig. 12, mandibular blade; fig. 13, maxillule; fig. 14, maxilla; fig. 15, maxilliped; fig. 16, first leg; fig. 17, second leg; fig. 18, third leg; fig. 19, fourth leg; fig. 20, fifth pair of legs posterior aspect.

exopod is 8-segmented, and the endopod 2-segmented. The first segment of the endopod is about 2.5 times as long as the second.

The mandibular palp (fig. 11) is slender and lacks setae on the basis. The endopod is slightly longer than the exopod. The cutting edge (fig. 12) of the mandibular blade consists of 2 strong rostral teeth, the inner of which has 2 small acute teeth along the internal margin and another along the external margin.

In the maxillule (fig. 13), the first inner lobe and the exopod are elongate. The first inner lobe has distally 7 spiniform setae, 2 of which are notably strong. The second and third inner lobes are small, and have 1 and 3 setae, respectively.

The maxilla (fig. 14) bears 6 well-developed lobes. The first lobe has 3 setae, each of the second to fourth lobes 2 setae, the fifth lobe 1 seta plus 1 strong spine, and the sixth lobe 2 setae plus 1 strong spine. The spine of the sixth lobe is slightly smaller than that of the fifth lobe. The endopod is 3-segmented and has 7 setae.

The coxa of the maxilliped (fig. 15) has 3 lobes, which have 2, 3, and 3 setae, respectively. The basis has 2 lobes, each with 2 setae. The endopod is 5-segmented; the first and second segments each have 4 setae, the third and fourth have 3, and the fifth has 4.

The basipod of the first leg (fig. 16) has 1 internal seta on the coxa and 1 external seta on the basis. Both the exopod and the endopod are 3-segmented. The first and second exopodal segments each have 1 internal seta and 1 external spine. The external spine of the first segment is notably long, extending beyond the end of the spine on the second segment. The third exopodal segment has 2 external spines, 4 internal setae, and 1 terminal spine. The endopod is about as long as the first 2 exopodal segments combined and has 1 seta on the first segment, 2 on the second, and 5 on the third.

The second to fourth pairs of legs (figs. 17-19) are similar. The coxa has 1 internal seta. The basis is naked in the second and third legs but has an external seta in the fourth leg. The exopod is 3-segmented; the first and second segments each have 1 external spine and 1 internal seta; and the third segment has 3 external spines, 5 internal setae, and 1 terminal

spine. The endopod is also 3-segmented. The first segment bears 1 seta, and the second segment 2 setae. The third segments of the second and fourth legs have 7 setae, but that of the third leg has 8 setae.

The fifth pair of legs (fig. 20) is asymmetrical. The coxa of the left leg has a strong tooth on the internal margin. The basis in both the right and the left legs has a long plumose external seta. The second exopodal segment of the right leg has a large, conical protrusion on the internal margin. The right and left third exopodal segments both have 2 external spines and 1 large terminal spine; the first external spine of the right third exopodal segment is spinose and as long as the terminal spine. The endopods of both legs are 3-segmented; the first segment lacks setae, but the second and third segments have 1 seta and 6 setae, respectively.

Remarks

The present specimens are in full agreement with the description by Giesbrecht (1892) except for the urosome, which seems to be somewhat shorter than that figured by him. This difference may be due to the telescoping of the segments. The female is not known.

Haloptilus spiniceps (Giesbrecht, 1892)

Occurrence

Sta. 3. 6 adult females, 4.41 to 4.80 mm.

Sta. 5. 5 adult females, 4.12 to 4.99 mm.

Sta. 7. 2 adult females, 4.50 to 4.60 mm.

Remarks

This species can readily be distinguished from the other species of the genus by the short, hooked, spiniform projection of the forehead, viewed from the side.

Augaptilus spinifrons Sars, 1907 (Plate 12, figs. 1-5)

Occurrence

Sta. 5. 1 adult female, 3.55 mm.

Remarks

The female of this species can be identified by five characters: The anterior end of the body is produced into an acute spiniform process that is pointed downward (figs. 1 and 2)—

the tip of the process appears to be divided into two minute points. The rostrum consists of two slender filaments. The mandibular palp (fig. 3) is uniramous and has 4 segments; the distal segment has 2 long plumose setae. The mandibular blade is armed with 5 rostral teeth (fig. 4). The fifth leg (fig. 5) has a long seta on the posterior surface of the basis that extends beyond the end of the exopod. This seta is much longer than that figured by Sars (1925).

This species has been recorded from the Azores and off Gibraltar by Sars (1907, 1925) and from the Great Barrier Reef by Farran (1936).

FAMILY ARIETELLIDAE

Arietellus aculeatus (T. Scott, 1894)
(Plate 12, figs. 6–16)

Rhincalanus aculeatus T. Scott, 1894, p. 31, plate 2, figs. 11–24.

Arietellus setosus Giesbrecht and Schmeil, 1898, p. 124.

Arietellus aculeatus, A. Scott, 1909, p. 143, plate 44, figs. 4–7; Farran, 1929, p. 270; Wilson, 1950, p. 165.

Occurrence

Sta. 3. 1 adult male, 3.60 mm.;
1 fifth copepodid male, 2.90 mm.

This species was originally erected on the basis of a single immature male from the Gulf of Guinea and placed in the genus *Rhincalanus* (T. Scott, 1894). Afterward it was made a synonym of *Arietellus setosus* by Giesbrecht and Schmeil (1898). A. Scott (1909) found a single mature female in the *Siboga* plankton. Upon this female and the immature male, A. Scott reestablished his father's species. Farran (1929) reported a mature male from off New Zealand but gave no detailed description. The following description is from an adult male referable to this species in the present collections.

Description of Male

The total length is 3.60 mm. The proportions of the prosome to the urosome are 4:1. The first metasomal segment is separated from the cephalosome, but the fourth and fifth metasomal segments are completely fused. The fore-

head has a very strong spiniform process, which is curved slightly downward in lateral aspect (fig. 7). The rostrum is composed of two slender filaments, which are almost hidden between the basal portions of the antennules. The spiniform projections of the last metasomal segments are slightly asymmetrical and rather divergent, but the tips are curved slightly inward. Of these projections the right one is slightly longer, reaching to the middle of the fourth urosomal segment (fig. 6). The urosome is 5-segmented; the second to fourth segments are of nearly equal length.

The left antennule is modified for grasping the female and is 19-segmented. Figure 8 shows the arrangement of the setae and aesthetes.

The antenna (fig. 9) is composed of a rather small basipod, a 2-segmented endopod, and a 6-segmented exopod. The endopod is longer than the exopod; both are slender.

The mandibular palp (fig. 10) lacks an endopod; the basis is longer than the exopod. The mandibular blade (fig. 11) is armed with 4 large teeth, 3 of which are grouped.

The maxillule (fig. 12) has 2 inner lobes, of which the first has 5 spines and the second a single spine. The single outer lobe has 8 setae. The exopod is relatively large, with 3 setae at the apex. The endopod is absent.

The maxilla and maxilliped are similar to those of *A. setosus* as figured by Giesbrecht (1892).

The coxa in the first pair of legs (fig. 13) has an internal seta, and the basis has an internal and an external seta. The endopod is 3-segmented; the first segment has 1 internal seta, the second segment 2 internal setae, and the third segment 2 internal setae, 1 external seta, and 2 terminal setae. The exopod is also 3-segmented; the first and second segments each have 1 external spine and 1 internal seta. The third segment has 4 internal setae, 2 external spines, and a terminal spine.

The basipod of the second leg (fig. 14) has a single seta on the internal margin of the coxa. The endopod is 3-segmented; it has 1 internal seta on the first segment, 2 internal setae on the second segment, and 8 setae on the third segment. The exopod is also 3-segmented; the first and second segments each have 1 internal seta and 1 slender, curved external spine. The

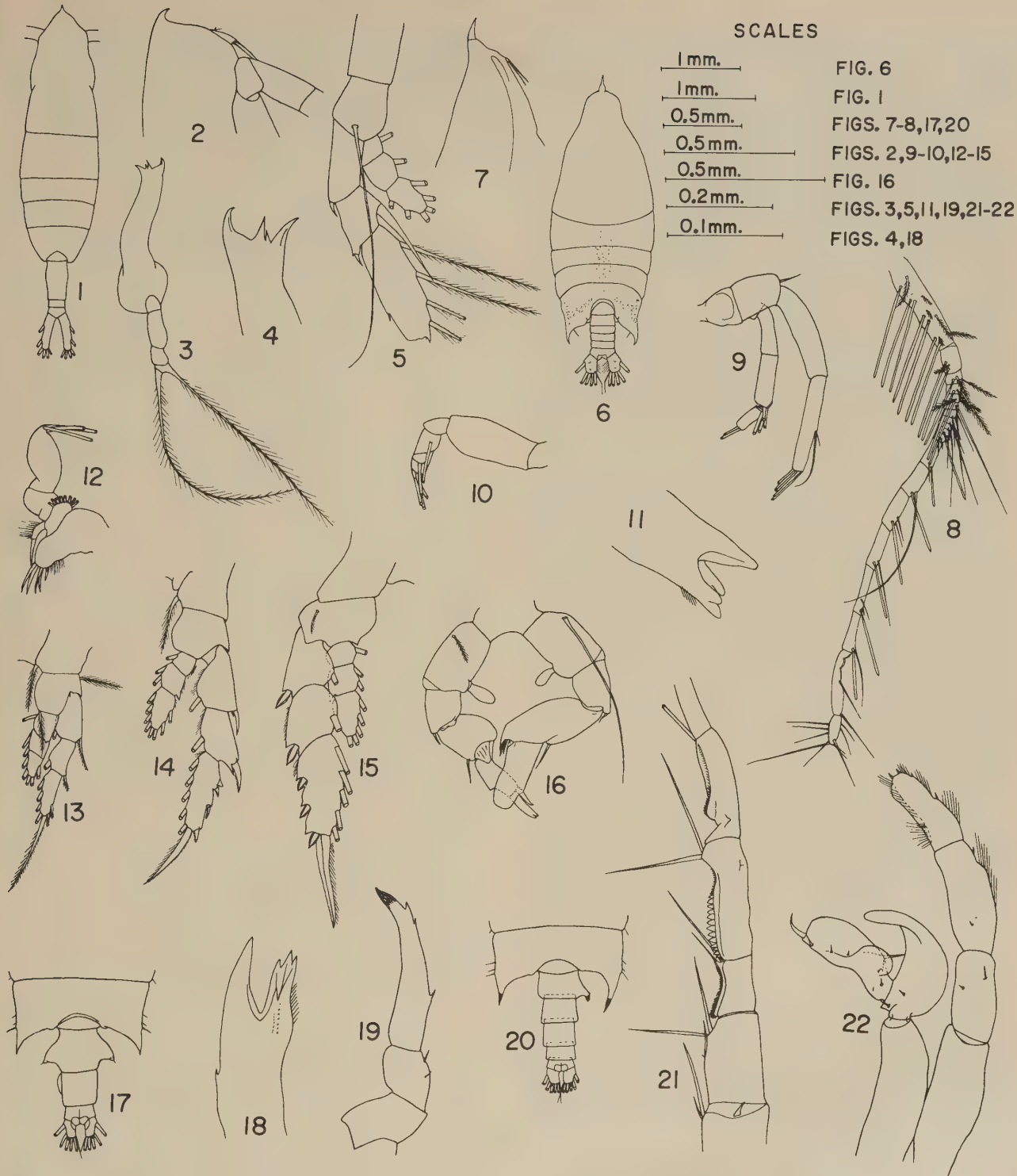


PLATE 12. Figs. 1-5, *Augaptilus spinifrons*. Female: fig. 1, habitus, dorsal view; fig. 2, forehead, lateral view; fig. 3, mandible; fig. 4, mandibular blade; fig. 5, fifth leg. Figs. 6-16, *Arietellus aculeatus*. Male: fig. 6, habitus, dorsal view; fig. 7, forehead, lateral view; fig. 8, left antennule; fig. 9, antenna; fig. 10, mandibular palp; fig. 11, mandibular blade; fig. 12, maxillule; fig. 13, first leg; fig. 14, second leg; fig. 15,

fourth leg; fig. 16, fifth pair of legs, posterior aspect. Figs. 17-22, *Candacia bipinnata*. Female: fig. 17, posterior part of metasome and urosome, dorsal view; fig. 18, mandibular blade; fig. 19, fifth leg. Male: fig. 20, posterior part of metasome and urosome, dorsal view; fig. 21, geniculated region of right antennule; fig. 22, fifth pair of legs, posterior aspect.

third segment has 5 internal setae, 3 small external spines, and 1 strong terminal spine almost as long as the segment.

The third and fourth legs (fig. 15) are similar. The basipod has a single seta on the posterior surface of the basis. The exopod is 3-segmented; the first and second segments each have 1 internal seta and 1 external spine; the third segment has 5 internal setae, 3 external spines, and 1 strong terminal spine nearly as long as the segment. The endopod is also 3-segmented; the first segment has 1 internal seta, and the second segment 2 internal setae. The number of setae on the third segment is 8 in the third leg and 7 in the fourth leg.

The fifth pair of legs (fig. 16) is asymmetrical. Both the right and the left legs have a 3-segmented exopod and a small, lamelliform endopod. The endopods of both legs have nearly the same shape, but the left one is slightly larger. The third exopodal segment of the left leg has a low, triangular projection on the external margin and 2 apical clawlike spines, the outer of which is larger and terminates with 2 points. The third exopodal segment of the right leg is lamelliform and lacks spines or setae.

Remarks

Because of one long frontal spiniform process, *A. aculeatus* appears to be closely related to *A. armatus* Wolfenden, 1911, which Farran (1929) considered as a probable synonym of the former. Wilson (1950), however, redescribed both sexes of *A. armatus* as a valid species.

The present specimen seems to differ only slightly from *A. armatus* described by either Wolfenden (1911) or Wilson (1950) in that the frontal process is comparatively short and both endopods of the fifth pair of legs are simple instead of forked.

Arietellus setosus Giesbrecht, 1892

Occurrence

Sta. 5. 1 adult male, 3.93 mm.

Sta. 7. 2 adult males, 4.03 to 4.12 mm.

Remarks

This species can readily be distinguished

from the other species of the genus by the short and slightly curved spiniform process of the forehead and the strong spiniform projections of the last metasomal segment. These characters have been figured by Grice (1962).

FAMILY CANDACIIDAE

Candacia ethiopica Dana, 1849

Occurrence

Sta. 3. 2 adult females, 2.47 to 2.60 mm.;
2 adult males, 2.48 to 2.50 mm.

Sta. 5. 3 adult females, 2.83 to 2.97 mm.;
5 adult males, 2.47 to 2.93 mm.

Sta. 7. 5 adult females, 2.77 to 3.03 mm.;
7 adult males, 2.50 to 2.67 mm.

Sta. 9. 1 adult female, 3.00 mm.

Remarks

The female is easily distinguished from the other species of the genus by the small lateral and ventral spiniform processes of the genital segment and by the terminal segment of the fifth leg, which has 7 spines.

The male is recognized by the spiniform projection of the left posterolateral corner of the metasome; the tip of this projection is divided into 2 points. The genital segment has 2 triangular processes on the right margin. These characters have been figured by Grice (1962).

Candacia bipinnata Giesbrecht, 1889 (Plate 12, figs. 17-22)

Occurrence

Sta. 13. 3 adult females, 2.90 to 3.00 mm.;
3 adult males, 2.77 to 2.83 mm.

Sta. 15. 3 adult females, 2.84 to 2.90 mm.;
2 adult males, 2.86 to 2.94 mm.

Sta. 16. 3 adult females, 3.06 to 3.16 mm.;
5 adult males, 2.75 to 3.02 mm.

Remarks

The genital segment of the female (fig. 17) has lateral conical projections; the tips of the projections are produced into small spines. The second urosomal segment has a flaplike protrusion on the ventral margin. The male is distinguished from the other species of the genus by the shape of the last metasomal segment and the genital segment (fig. 20).

Occurrence

Sta. 3. 1 adult female, 2.50 mm.

Sta. 7. 1 adult female, 2.80 mm.

Remarks

The female is recognized by the symmetrical genital segment, the fifth pair of legs, and the shape of the mandibular blade (see Grice, 1962, plate 31, figs. 8, 10, and 13).

Candacia longimana Claus, 1863

Occurrence

Sta. 3. 1 adult male, 3.19 mm.

Sta. 5. 1 adult male, 3.20 mm.

Sta. 7. 1 adult male, 3.55 mm.

Remarks

The male of this species can be identified by the spiniform process on the right posterolateral margin of the metasome, the conical process on the right margin of the genital segment, and the structure of the fifth pair of legs (see Grice, 1962, plate 28, figs. 6, 8, 11, and 12).

Paracandacia bispinosa (Claus, 1863)

Occurrence

Sta. 3. 14 adult females, 1.74 to 1.91 mm.;
12 adult males, 1.88 to 1.94 mm.

Sta. 5. 20 adult females, 1.74 to 2.01 mm.;
17 adult males, 1.94 to 2.11 mm.

Sta. 7. 9 adult females, 1.84 to 1.91 mm.;
5 adult males, 2.04 to 2.11 mm.

Remarks

This species is one of the most common from the southern stations. The genital segment of the female is nearly triangular when viewed from above. Each side of the segment is produced into a small spine; the spine of the left side is longer and directed backward. The male can be distinguished by the shape of the geniculated portion of the right antennule. These characters have been figured by Grice (1962).

The species was transferred by Grice (1963) from the genus *Candacia* to his new genus *Paracandacia*.

Pontellopsis regalis (Dana, 1849)

(Plate 13, figs. 1-14)

Occurrence

Sta. 3. 1 adult female, 3.20 mm.

Description of Female

The total length is 3.20 mm. The ratio of the prosome to the urosome is 4.6:1. The first metasomal segment is separated from the cephalosome. The forehead in dorsal aspect (fig. 1) is broadly rounded and has a projection over the base of the rostrum. The last metasomal segment, consisting of the fused fourth and fifth metasomal segments, is produced posterolaterally into acute spiniform processes directed backward. In dorsal aspect these processes appear to reach two-thirds the length of the genital segment (fig. 2).

The urosome is 2-segmented. The genital segment in dorsal aspect is slightly asymmetrical. Its width increases toward the posterior margin, where each side is projected posteriorly into a conical process; the right process is shorter than the left and has a minute, spiniform bristle at the apex. The anal segment and the caudal rami are symmetrical; their combined length is slightly shorter than the genital segment.

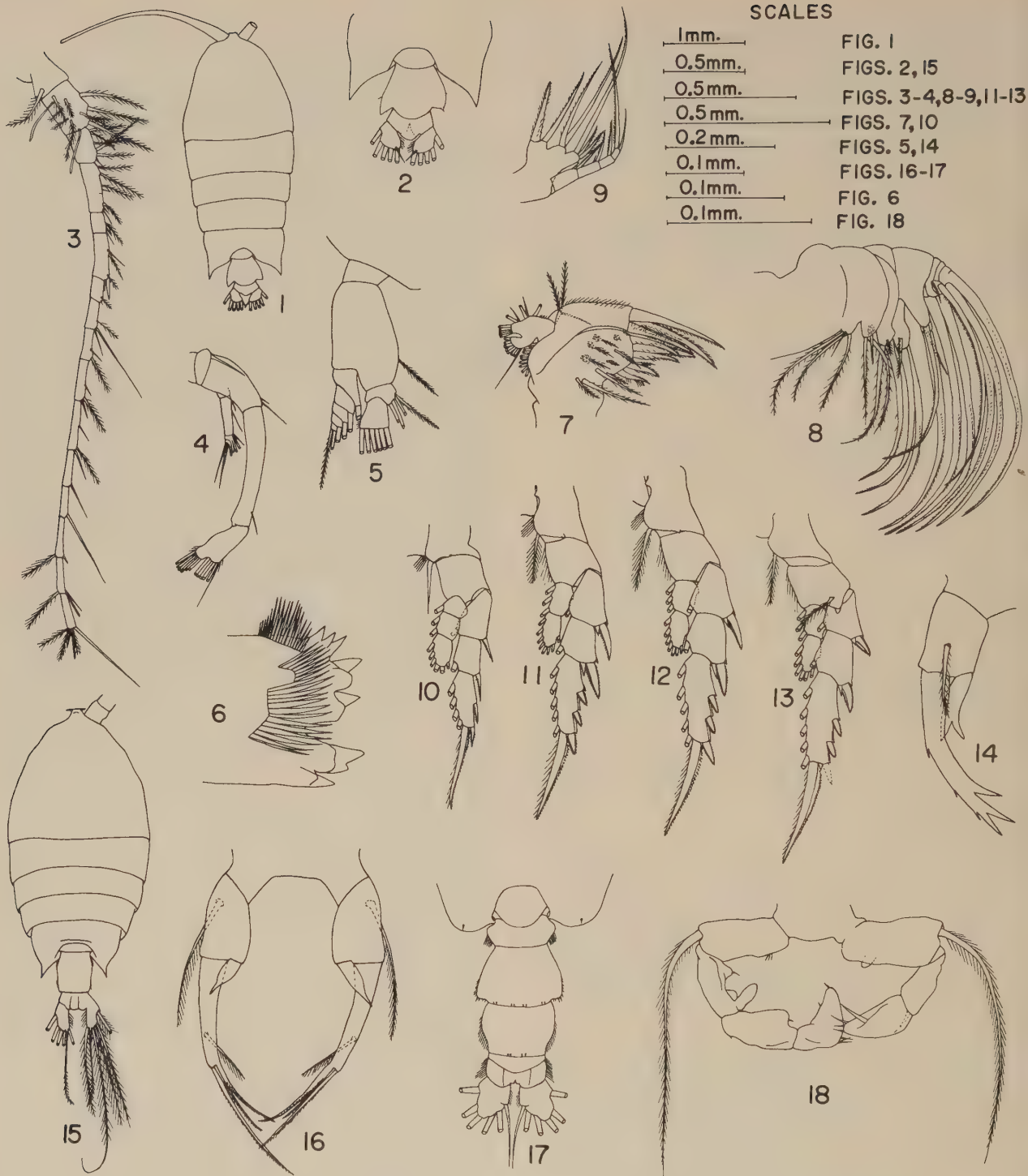
The antennule (fig. 3) is 16-segmented and reaches the middle of the second metasomal segment. The exopod of the antenna (fig. 4) is very small—about one-third the length of the endopod.

The mandibular blade (fig. 6) has five groups of teeth, in addition to three rows of strong spines on each side.

The first and second inner lobes of the maxillule (fig. 7) are well developed; the first has 6 spines along the internal margin and 10 on the posterior surface, and the second has 3 strong spines on the tip. The third inner lobe is small; it has 3 setae. The basis, endopod, and exopod are fused.

The maxilla (fig. 8) is strongly developed and has 5 lobes on the basipod. The endopod has 6 strong spines plus 1 small spine.

The maxilliped (fig. 9) consists of 1-segmented basipod and a 4-segmented endopod.



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PLATE 13. Figs. 1-14, *Pontellopsis regalis*. Female: fig. 1, habitus, dorsal view; fig. 2, posterior part of metasome and urosome, dorsal view; fig. 3, antennule; fig. 4, antenna; fig. 5, mandibular palp; fig. 6, mandibular blade; fig. 7, maxillule; fig. 8, maxilla; fig. 9, maxilliped; fig. 10, first leg; fig. 11, second leg; fig. 12,

third leg; fig. 13, fourth leg; fig. 14, fifth leg. Figs. 15-16, *Pontellina plumata*. Female: fig. 15, habitus, dorsal view; fig. 16, fifth pair of legs. Figs. 17-18, *Acartia negligens*. Male: fig. 17, posterior part of metasome and urosome, dorsal view; fig. 18, fifth pair of legs.

The basipod is broad and has 3 lobes, which have 2, 2, 3 spines, respectively.

The basipod of the first leg (fig. 10) has a single seta on the internal margin of the coxa. The exopod is 3-segmented. Each of the first and second segments has an internal seta and an external spine. The third segment has 2 external spines, 4 internal setae, and a terminal spine that is serrated along the outer margin. The endopod is also 3-segmented. The first segment has a single internal seta, the second segment 2 internal setae, and the third segment 6 setae.

The second and third pairs of legs (figs. 11 and 12) are similar. The basipod carries a single internal seta on the coxa. The exopod is 3-segmented. Each of the first and second segments has an internal seta and a strong external spine. The third segment has 3 external spines, 5 internal setae, and a strong terminal spine that is serrated along the external margin. The endopod is 2-segmented. The first segment has 3 internal setae and 1 external seta. The second segment has 8 setae.

The fourth pair of legs (fig. 13) is similar to the third, but the basis has a seta on the posterior surface and the second endopodal segment has 7 setae instead of 8.

The basipod of the fifth leg (fig. 14) has a plumose seta on the posterior surface of the basis. The exopod and endopod each consist of a single segment. The exopod has a forked tip, a strong spine along the internal margin, and 3 small spines along the external margin. The endopod also has a forked tip; it is about one-third the length of the exopod.

Remarks

In the shape of the urosome the present specimen is not in full agreement with the description given by Giesbrecht (1892). According to A. Fleminger (personal communication), however, it is not outside the usual variability shown by the species.

Pontellina plumata (Dana, 1849)
(Plate 13, figs. 15-16)

Occurrence

Sta. 7. 1 adult female, 1.94 mm.

Remarks

A single female referable to the above species was in the present collections. The specimen agrees in every detail with the description and figures given by Giesbrecht (1892) except for the structure of the endopod of the fifth leg (fig. 16). The sizes of the right and left endopods are slightly unequal, and each is single-pointed, not forked.

FAMILY ACARTIIDAE

Acartia danae Giesbrecht, 1889

Occurrence

Sta. 3. 1 adult female, 1.20 mm.

Remarks

The female can be recognized by the large spine on the first segment of the antennule, the pointed posterolateral corners of the metasome, and the structure of the fifth pair of legs.

Acartia negligens Dana, 1849
(Plate 13, figs. 17-18)

Occurrence

Sta. 3. 3 adult females, 1.23 to 1.30 mm.

Sta. 5. 5 adult females, 1.22 to 1.28 mm.;
1 adult male, 1.15 mm.

Sta. 7. 7 adult females, 1.25 to 1.28 mm.;
1 adult male, 1.18 mm.

Remarks

In the female, the fifth pair of legs is somewhat similar to that of *A. danae*, but the posterolateral corners of the metasome are rounded and have small spines. The shape of the urosome and the fifth pair of legs of the male can best be described by reference to figures 17 and 18.

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A RAPID METHOD OF TAGGING FISH¹

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A unique tagging procedure has been devised that requires but two persons, is rapid, and provides accurate permanent records that can be rechecked as many times as necessary. Methods used up to this time require several men, and the records obtained are only temporary and often inaccurate.

The Division of Fish and Game, Department of Land and Natural Resources, State of Hawaii, is now tagging akule (bigeye scad), *Trachurus crumenophthalmus*, for studies of growth and migration.

Generally, our tagging method is an extension and modification of fish measuring techniques described by Wollaston (1928), Thompson (1929), and recently by Joeris (1959), who used a measuring board to which plastic strips (exposed or outdated X-ray film strips) were attached. The fish is laid on the measuring board with its snout against a stopblock, and the length is recorded by punching a hole in the film. The method described here involves the same general technique except that X-ray films are also specially prepared to hold and dispense tags in numerical order and to retain paired information on tag numbers and length of fish tagged.

The adaptation of X-ray film to fulfill the method's requirements was accomplished by painting stripes on the film and placing a tag with each stripe. It involves the association of tag, tag number, and length of fish represented by a perforation on the film in the striped area. To adapt the film, each exposed X-ray film plate (obtained from local hospitals without cost) is prepared with several equally spaced horizontal 12.5-mm. wide yellow stripes spray-painted through a template on the film. At the end of each stripe the film is slit to hold the modified plastic internal anchor tag used on *T. crumenophthalmus* (Sakuda, 1966);

the tags are in numerical order from the top to the bottom of the film. The tag numbers are written on the first and last stripes with a china-marking pencil (fig. 1). The size of the X-ray film, number of stripes, and spacing between stripes, depend on the size of fish to be tagged. For akule, a plate 36.0 by 43.2 cm. is used; it carries 15 stripes. Other types of tags (e.g. dart, spaghetti, or Petersen disk) may be attached to the tagging plate with masking tape.

The tagging plates require a flat surface for their use; a table with a 12.5-mm.-thick cork top and a stopblock along one edge served this purpose. The tagging plate is butted firmly against the stopblock and securely pinned to the table, and the immobilized fish is laid along the horizontal stripe with its snout against the stopblock. Length is then recorded by perforating the stripe with a dissecting needle. The corresponding tag at the end of the stripe is then removed from the plate and inserted into the body cavity through a small incision on the side of the fish.

To minimize handling of the fish, a holder is also used in the tagging. It is constructed of 1.5-mm.-thick clear plastic sheet, 30.5 cm. long and 6.3 cm. wide, with a 12.5-mm.-wide lengthwise slot to match the horizontal stripe on the tagging plate. When placed over the tagging plate, the holder is manipulated to center the fish over the stripe and in position for the length measurement to be punched. A 6.2-mm.-thick sheet of polyurethane foam, 23.0 cm. long and 6.3 cm. wide, is glued to the upper surface of the holder to provide a soft, moist bed for the fish during tagging. A piece of nylon window screen the size of the holder is glued to the undersurface of the holder to reduce adhesion of the holder to the tagging plate. Fish length is recorded by punching a hole into the tagging plate through the foam sheet and screen.

The tagging plates are stored in numerical order in cardboard boxes painted with epoxy resin. Upon completion of a day's tagging, the

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FIGURE 1.—The fish tagging equipment in use.

plates are washed and dried, and tag numbers and length measurements are recorded. Fish lengths are read off the tagging plates with a T-square ruler.

With experience in judging the time required to immobilize akule, two men (a tagger and an anesthetist) have tagged about 100 fish per hour. The rapidity and relative ease of tagging by this method also afford time for additional care in

handling the fish. Use of the X-ray-film tagging plate has three other advantages over the usual tagging procedure: it (1) eliminates reading and recording the tag numbers and fish-length measurements during the tagging; (2) minimizes errors (misreading, misrecording, and digit bias) during the tagging; and (3) provides permanent length records that can be rechecked later.

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MIGRATION AND DISTRIBUTION OF PINK SALMON SPAWNERS IN SASHIN CREEK IN 1965, AND SURVIVAL OF THEIR PROGENY

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ABSTRACT

The escapement of 14,813 pink salmon (*Oncorhynchus gorbuscha*) to Sashin Creek, southeastern Alaska, in 1965, followed by the emergence of 2.2 million fry, or 18 percent of the potential egg deposition, represented a relatively high survival of eggs and alevins in a stream, where the long-term average is 7 percent. This high survival was predicted from an established relation between survival of eggs and alevins and the time the parents entered Sashin Creek to spawn.

The spawning ground was divided into three areas—upper, middle, and lower—to study density of spawners and survival of their progeny. Density in 1965 was higher in the middle and upper areas than in the lower. From egg deposition to fry emergence, survival was estimated

to be 23 percent in the upper area, 18 percent in the middle area, and 14 percent in the lower area.

The instantaneous rate of mortality remained relatively unchanged from deposition of eggs to emergence of fry in the upper and middle areas. In the lower area, mortality was relatively high during spawning and low between spawning and hatching of eggs. Much of the mortality throughout the stream was traced to the disappearance of eggs and alevins. Factors causing this disappearance included retention of eggs, superimposition of redds, predation, and turbulent water. A drought during spawning retarded development of embryos and caused considerable mortality.

The numbers of pink salmon (*Oncorhynchus gorbuscha*) fluctuate drastically from year to year, and knowledge of the natural processes that cause the fluctuations is required if the resource is to be managed effectively. To evaluate mortality of pink salmon in fresh water, the Bureau of Commercial Fisheries has studies in Sashin Creek, a small spawning stream on Baranof Island, southeastern Alaska.

Adult pink salmon entering Sashin Creek have been counted each year since 1934, and fry leaving have been counted since 1941. Adults have numbered from 8 to 92,085 and fry from 50 to 5,940,300; fresh-water survival has ranged from 0.06 to 21.75 percent of potential egg deposition (table 1).

Only a small portion of Sashin Creek can be used by salmon spawners. Although the Creek is about 4,000 m. long, a waterfall 1,200 m. from the head of tidewater prevents further upstream movement of fish. Spawning is limited in a narrow canyon that extends 300 m. downstream from the waterfall and in the intertidal zone, where the gradient is steep and the bottom is mostly bedrock. The main spawning ground (13,629 m.²) lies between the intertidal zone and the canyon.

Four factors that affect survival of pink salmon in Sashin Creek have been discussed by Merrell (1962) and McNeil (1966): (1) time of migration of spawners, (2) distribution of spawners, (3) density of spawners, and (4) weather. To clarify further the relation of these and possibly other factors to survival of eggs, alevins, and fry in Sashin Creek, I studied a relatively large run of pink salmon that spawned there in late August and in September 1965. Survival from deposition of eggs to emergence of fry was estimated in three areas that included 97 percent of the total spawning ground used by spawners in years of large escapements.

In this paper, I describe the migration, distribution, and density of pink salmon spawners in the summer of 1965, and the survival of their progeny in fresh water. Also, I discuss: (1) the relation of survival of eggs and alevins to time of spawning of adults, (2) variation among stream areas in density of fry, (3) relation of water quality (primarily concentration of dissolved oxygen) to survival and development of embryos, (4) disappearance of eggs and alevins from spawning beds, and (5) seasonal variation in mortality in spawning beds.

TABLE 1.—Number of adult pink salmon in each escapement, potential egg deposition, number of fry produced, and fresh-water survival for brood years 1934–65, Sashin Creek, southeastern Alaska

Brood year ¹	Adults in escapement	Potential egg deposition ²	Fry produced	Fresh-water survival
	Number	Number	Number	Percent
1934	7,917			
1935	6,323			
1936	5,364			
1937	9,085			
1938	6,467			
1939	16,830			
1940	53,594	52,858,000	3,399,900	6.43
1941	84,303	88,678,000	1,024,300	1.16
1942	92,085	78,894,000	674,000	0.85
1943	14,883	14,980,000	227,800	1.52
1944	4,050	3,904,000	105,600	2.71
1945	5,465	5,062,000	43,100	.85
1946	933	736,000	1,200	.16
1947	1,486	1,330,000	27,600	2.07
1948	597	516,000	9,100	1.76
1949	4,902	4,800,000	176,200	3.67
1950	112	86,000	50	.06
1951	4,366	4,062,000	412,500	10.15
1952	45	(³)	740	—
1953	1,164	1,284,000	95,400	7.43
1954	21	12,000	660	5.48
1955	9,267	10,286,000	266,200	12.31
1956	933	1,018,000	5,040	.50
1957	2,834	2,588,000	562,900	21.75
1958	217	174,000	10,700	6.13
1959	35,391	40,379,000	5,332,400	13.21
1960	162	(³)	480	—
1961	28,759	29,425,000	5,940,300	20.19
1962	8	8,000	100	1.20
1963	16,757	16,640,000	3,256,300	19.57
1964	⁴ 2,193	2,230,000	⁵ 310,000	13.91
1965	14,833	12,668,000	⁵ 2,235,000	17.92

¹ The term "brood year" refers to the year of spawning.

² Based on 2,000 eggs per female except when actual fecundity was calculated in 1942 (1,936 eggs), 1957 (1,988 eggs), 1959 (2,040 eggs), 1960 (1,903 eggs), 1961 (1,991 eggs), 1963 (1,908 eggs), 1964 (1,709 eggs), and 1965 (1,782 eggs).

³ An attempt was made to destroy the spawners.

⁴ Natural escapement (327) was reinforced by introduction of 1,866 adults.

⁵ Fry weir was not functioning; estimate based on number of preemerged alevins in spawning beds.

MIGRATION, DISTRIBUTION, AND DENSITY OF SPAWNERS

Fresh-water survival of pink salmon eggs and alevins in Sashin Creek is inversely related to the time of migration of the spawners (Skud, 1958; Merrell, 1962). Because pink salmon are mature when they enter Sashin Creek, early entry into the stream means early spawning and late entry gives late spawning. The date by which 50 percent of all of the spawners had entered the Creek is used in this paper to index the time of spawning. In 1965, 50 percent of the spawners had entered the Creek by August 26, which was the fourth earliest date of record. I had expected, therefore, that survival of the eggs and alevins would be high.

The distribution and density of spawners in 1965 were analyzed to determine if spawners concentrated in areas that afforded the best habitat for embryos and alevins. Ninety-seven percent (13,084

m.²) of the Sashin Creek spawning ground was divided into three areas—upper (2,945 m.²), middle (4,067 m.²), and lower (6,072 m.²). The upper area has a relatively high gradient and coarse materials in the bed; the middle area has an intermediate gradient and medium-sized materials; and the lower area has a low gradient and relatively fine materials (table 2).

TABLE 2.—Average gradient and size composition of bottom materials¹ in three areas in Sashin Creek

Area	Average gradient	Bottom composed of—		
		Coarse particles ²	Medium particles ²	Fine particles ²
	Percent	Percent	Percent	Percent
Upper	0.7	81	16	3
Middle	.3	61	26	13
Lower	.1	47	36	17

¹ Procedures for sampling bed materials to measure size composition were described by McNeil and Ahnell (1964).

² Coarse particles are >12.7 mm. diameter; medium particles are 1.68 to 12.7 mm.; fine particles are <1.68 mm. diameter.

In years before 1965, when spawners were abundant they used the entire Sashin Creek spawning ground but concentrated in the middle area. Nevertheless, the upper area produced more fry per unit area of streambed than the middle or lower area (Merrell, 1962; McNeil, 1966). When spawners were scarce, they usually concentrated in the lower area and did not use the upper area at all. The failure of spawners to use the potentially most productive upper area raises important questions about factors that control their distribution.

In 1965, 14,813 pink salmon spawners, including 7,109 females, entered Sashin Creek. Two hundred of the females were captured as they passed the weir and were tagged with plastic Petersen disks 1.6 cm. in diameter, fastened below the dorsal fin. Fifty fish were tagged with white disks on August 18, 50 with red disks on August 24, 50 with yellow disks on August 28, and 50 with green disks on September 12. The dates of release of the tagged females were selected to ensure representation of the early, middle, and late portions of the migration to fresh water. Seven percent of the total number of females (7,109) had entered Sashin Creek before the first date of tagging (August 18); 37 percent before the second date (August 24); 70 percent before the third date (August 28); and 95 percent before the fourth date (September 12). An observer on foot

counted tagged and untagged females in each area and recorded their location. Only females were counted because they determine potential egg deposition.

The females were easy to count on the spawning ground because they remained near the site of their redds from the beginning of spawning until they died. I evaluated this behavior, which is typical of spawning females, by observing 14 tagged females that were spawning in a 100-m.-long section of Sashin Creek. The locations of the 14 females were determined twice daily with a transit and stadia and were plotted on a detailed map. The average longevity on the spawning ground of the 14 females was 11.5 days (range 3 to 20 days). The average size of the area occupied was 3.8 m.² (1.4 m. wide by 2.7 m. long). The smallest area occupied, 0.6 m.², was for a fish that lived only 3 days after establishing a site, and the largest, 17.3 m.², was for a fish that lived 9 days. All died near their redds.

One method of estimating the number of females that spawned in an area was to sum the daily counts of untagged females and divide by their average longevity. The daily counts were summed by fitting a curve to the number of untagged females counted each day and measuring the area under the curve (examples are given by McNeil, 1964a and 1964b). Average longevity was estimated from daily observations of tagged females. One day was added to the number of days individual tagged females were observed because I assumed they occupied the spawning ground one-half day before they were first observed and one-half day after they were last observed.

Estimates of the number of females in each area based on summed daily counts and average longevity were 2,040 in the upper area, 3,095 in the middle, and 3,051 in the lower. I assumed that 97 percent of the total number of females spawned in the three areas, and my estimate for the whole stream was 8,439 females, or 118.7 percent of the number counted at the weir. The estimates for each area were, therefore, adjusted by dividing by 1.187. The resulting estimates were 1,719 females in the upper area, 2,607 in the middle, and 2,570 in the lower.

A second method of estimating the number of females in each area was based on the occurrence of tagged females. I assumed that tagged and untagged females were distributed similarly. Of the

TABLE 3.—*Density of female pink salmon spawning in three areas of Sashin Creek, based on observations of untagged females (summed daily counts) and tagged females*

Area	Females per square meter, based on—		Mean of the two estimates
	Observations of untagged females	Observations of tagged females	
	Number	Number	Number
Upper.....	0.58	0.57	0.58
Middle.....	.64	.59	.62
Lower.....	.42	.46	.44

200 tagged females released, 184 (92 percent)¹ were recorded in the study areas: 45 in the upper area, 64 in the middle, and 75 in the lower. On the further assumption that 97 percent of the females counted at the weir spawned in the three areas and were distributed in the same proportion as the 184 tagged females, I estimated that 1,689 females spawned in the upper area, 2,399 in the middle, and 2,813 in the lower.

The density of females spawning in each area was calculated by dividing the total number of females by the area of spawning bed. The estimates of density of females in each area by each of the two methods for estimating the number of females agreed closely (table 3) and indicated that density of spawners was about the same in all areas. Although the observed number of tagged females in each area was not significantly different from the expected number calculated from an assumed uniform density of tagged females (table 4), the conclusion that the average density of females was identical among the areas is less attractive than the conclusion that small differences existed. I will use, therefore, the mean of the two estimates of density for each area (table 3) as the best (most probable) estimate of density in my calculations of potential egg deposition.

¹ Additional tagged females may have spawned in the study areas but were not seen.

TABLE 4.—*Numbers of tagged female pink salmon observed in three areas in Sashin Creek and the expected number, based on an assumed equal density*

Area	Female pink salmon	
	Observed	Expected
	Number	Number
Upper.....	45	41.4
Middle.....	64	57.2
Lower.....	75	85.4

$$\chi^2 (2 \text{ d.f.}) = 2.39 (P, 0.30).$$

SURVIVAL OF EGGS AND ALEVINS

Estimates of survival of eggs and alevins in this paper pertain to three periods in the freshwater life of 1965 brood year pink salmon:

Period	Months
1. Egg deposition (late August through September)-----	1. 3
2. Egg deposition and hatching (October through mid-November)-----	1. 7
3. Hatching and fry emergence (late November into late March)-----	4. 2
Total-----	7. 2

Survival in the n th period is calculated by:

$$S_1 \cdot S_2 \cdot \cdot \cdot S_n = S \quad (1)$$

$$S_n = \frac{S}{S_1 \cdot S_2 \cdot \cdot \cdot S_{(n-1)}} \quad (2)$$

The symbol S is total survival from beginning of spawning to any selected date, and an estimate of S ($\hat{S}$) must account for dead eggs and alevins that may have disappeared from the population before the date of sampling. The estimate must also give a value $\hat{S} \leq 1.0$. To satisfy these requirements, the estimate of survival is calculated from:

$$\hat{S}_j = \frac{\frac{1}{k} \sum_{i=1}^k T_{ij}}{e_j} \cdot \frac{\sum_{i=1}^k a_{ij}}{\sum_{i=1}^k T_{ij}} \quad (3)$$

with the condition that

$$\frac{\frac{1}{k} \sum_{i=1}^k T_{ij}}{e_j} \leq 1.0 \quad (4)$$

In equations (3) and (4),

- i designates an individual sampling ($i=1$ to k),
- j designates an individual area ($j=1$ to 3),
- a_{ij} is the number of live eggs and alevins collected at the i th point of the j th area,
- T_{ij} is the total number of eggs and alevins (live and dead) collected at the i th point of the j th area,
- e_j is the average potential egg deposition in the j th area, and
- $\hat{S}_j$ is an estimate of S for the j th area.

For the case where

$$\frac{\frac{1}{k} \sum_{i=1}^k T_{ij}}{e_j} < 1.0$$

equation (3) reduces to

$$\hat{S}_j = \frac{\frac{1}{k} \sum_{i=1}^k a_{ij}}{e_j} \quad (5)$$

I used equation (5) in an earlier paper (McNeil, 1966) to estimate survival of pink salmon in Sashin Creek:

The average density of eggs and alevins was estimated in each area from samples obtained with hydraulic sampling equipment described by McNeil (1964a). The points sampled, each representing 0.1 m.² of the streambed, were selected randomly within the three study areas with the aid of tables of random numbers. Eggs were collected after spawning (September 29), and eggs and alevins were collected during hatching (November 20) and before emergence (March 26).

In calculating $\hat{S}_j$ (equation 3 or 5), I assumed that the number of eggs collected at each point was 93 percent of the number actually present at the time of sampling (McNeil, 1964a). Potential egg deposition was calculated by multiplying the average fecundity by the estimated average number of females that had spawned per square meter (table 3). The average fecundity, based on 20 randomly selected unspawned females taken at the weir on the four dates females were tagged, was estimated to be 1,782 eggs.

Estimates of survival from August 20 (beginning of spawning) to September 29, November 20, and March 26 are given for each area in table 5. These estimates were calculated directly from equation (3).

The estimated number of eggs per square meter in the middle area at the end of spawning was greater than the estimated potential egg deposition (table 5). Two sources of error could have contributed to this discrepancy: (1) Potential egg deposition may have been underestimated, or (2) the number of eggs at the end of spawning may have been overestimated.

The use of an area by spawning salmon can be indexed in two ways—directly by observing the density of spawners (table 3) and indirectly by

TABLE 5.—*Potential egg deposition, number of live and dead eggs and alevins, ratio of live to combined live and dead eggs and alevins, and survival of 1965 brood pink salmon in three areas of Sashin Creek*

Area	Potential egg deposition per square meter		Period beginning August 20 and ending—	Eggs and alevins per square meter				Calculated survival
	Mean	90-percent confidence- limits of mean		Combined live and dead		Ratio of live to com- bined live and dead		
				Mean	90-percent confidence limits of mean	Mean	90-percent confidence limits of mean	
	Number	Number		Number	Number	Percent	Percent	Percent
Upper-----	1, 034	±72	September 29-----	966	±216	84	±5	78
			November 20-----	711	±191	86	±5	59
			March 26-----	433	±153	54	±16	23
Middle-----	1, 105	±77	September 29-----	1, 504	±312	86	±4	186
			November 20-----	765	±222	80	±8	55
			March 26-----	428	±112	47	±14	18
Lower-----	784	±55	September 29-----	539	±180	60	±16	241
			November 20-----	549	±214	71	±13	250
			March 26-----	357	±95	30	±13	14

¹ This estimate is uncorrected for egg retention. The estimate corrected for egg retention is 82 percent.

² These estimates do not differ significantly and are averaged to give 46 percent survival for each date.

measuring the presence of eggs in sampling units at the end of spawning. To measure the presence of eggs, I classified samples with more than three eggs and alevins as points used by spawners and those with fewer eggs as unused. The classification of sample points with three or fewer eggs and alevins as unused is arbitrary, but some small value greater than zero helps correct for the presence of drifted eggs at points not actually used by spawners.

It is probable that the density of eggs in the middle area at the end of spawning was overestimated. The percentage of samples containing more than three eggs and alevins (table 6) did not change significantly for any area from immediately after spawning (September 29) to hatching (November 20). The percentages of samples with more than three eggs or alevins were similar in the upper and middle areas in both September and November, and these similar measures of use in the two areas agree with observed densities of females. Furthermore, the upper and middle areas were similar in terms of the density of eggs and alevins in both November and March (table 5). The potential egg deposition was also about equal in the two areas, and together these observations support strongly the conclusion that density of eggs was overestimated in the middle area at the end of spawning.

Relatively few eggs were unspawned in the body cavities of females. Spawned females retained 5 percent of the potential egg deposition (based on an examination of 173 females).

TABLE 6.—*Percentage of 0.1 m.² sampling units in three areas in Sashin Creek with more than three eggs and alevins, after spawning and during hatching*

Study area	Sampling units with more than three eggs or alevins—			
	After spawning (September 29)		During hatching (November 20)	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
	Percent	Percent	Percent	Percent
Upper.....	66	±8	68	±9
Middle.....	73	±7	68	±9
Lower.....	50	±8	47	±10

Estimates of survival at the end of spawning include allowance for 5 percent retention of eggs by females in the upper and lower areas. In the middle area, however, the density of live and dead eggs at the end of spawning was calculated to be 100 percent of potential egg deposition (equation 3). This estimate is too high and requires further correction for the retention of eggs by females. Because only 95 percent of potential egg deposition was voided during spawning, the estimated 86 percent of live eggs in the middle study area in late September (table 5) pertains to 95 percent (or less) of potential egg deposition. The survival estimate corrected for egg retention is, therefore,

$$0.95 \times 0.86 = 82 \text{ percent.}$$

Correction is also required for two estimates of survival in the lower area where survival was estimated to increase from 41 percent in September to

50 percent in November. Because the difference between 41 and 50 percent survival is not statistically significant, I assume that no mortality occurred in the lower area between September 29 and November 20 and use the average of the two estimates, 46 percent survival, for the spawning period through November 20.

Equation (2) was used to calculate survival in each period. Table 7 gives the results of these calculations.

Instantaneous mortality coefficients corresponding to survival percentages given in table 7 were also calculated. The equation (McNeil, 1966) is:

$$M_{jn} = \frac{-\ln(S_{jn})}{t} \quad (6)$$

where M_{jn} is the mortality coefficient for the j th area and n th period,

S_{jn} is survival for the j th area and n th period, and

t is time.

In computing values of M , the unit of time is taken as 1 month. Thus, $t=1.3$ for period 1; 1.7 for period 2; and 4.2 for period 3. The values of M for each area and period are given in table 8.

TABLE 7.—Survival of pink salmon of the 1966 brood year in three areas in Sashin Creek

Study area	Survival from—			Total survival
	Potential egg deposition to actual egg deposition (period 1)	Actual deposition to hatching (period 2)	Hatching to emergence (period 3)	
	Percent	Percent	Percent	Percent
Upper.....	78	76	39	23
Middle.....	82	67	33	18
Lower.....	46	100	30	14

TABLE 8.—Instantaneous mortality coefficients for pink salmon of the 1966 brood year in three areas in Sashin Creek

Area	Instantaneous mortality coefficient from—		
	Potential egg deposition to actual egg deposition (period 1)	Actual deposition to hatching (period 2)	Hatching to emergence (period 3)
Upper.....	0.19	0.16	0.23
Middle.....	.20	.24	.29
Lower.....	.60	.00	.30

Changes in the number of live eggs and alevins in each area and in the entire stream are shown in figure 1. The numbers declined in the upper and

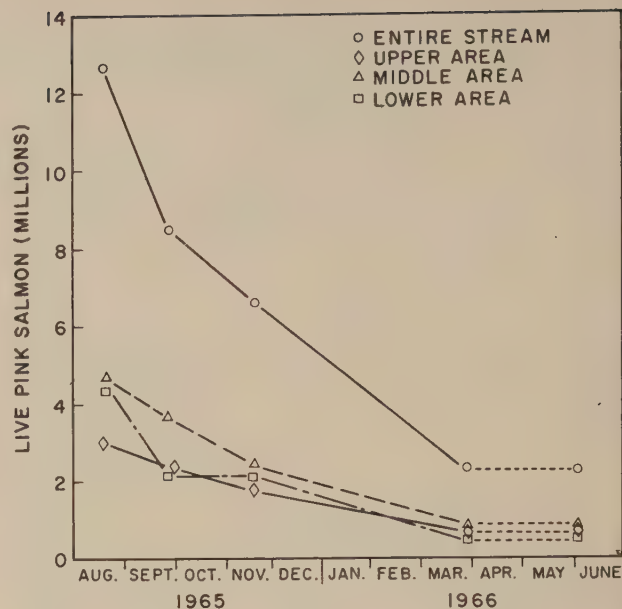


FIGURE 1.—Number of live pink salmon of the 1965 brood year in three areas of Sashin Creek and in the entire stream at beginning and end of four periods in fresh water. The dotted extensions in April and May are for the period of fry migration and are discussed in the text.

middle areas at nearly uniform rates in periods 1, 2, and 3. In the lower area, the numbers declined sharply in periods 1 and 3 but did not decline in period 2. Fry were not counted at the weir in the spring of 1966 because it had been damaged in late winter, but I have assigned 100-percent survival to period 4 (dotted extensions of the curves in figure 1) in all areas on the basis of previous years' data from Sashin Creek (table 9).

Although the density of fry varied among the three areas, the number of fry produced in each was about the same because of differences in sizes

TABLE 9.—Comparison of estimates of survival of pink salmon fry in Sashin Creek before the fry emerge (hydraulic sampler) and at the time they migrate (weir), 1959-63

Brood year	Estimates of survival	
	Hydraulic sampler	Weir
	Percent	Percent
1959.....	11.0	13.2
1960.....	(1)	
1961.....	21.4	20.2
1962.....	0.0	1.2
1963.....	20.7	19.6
Mean.....	13.3	13.6

(1) No estimate.

of the areas. The upper area had the highest number per square meter (228), the middle area the next highest (197), and the lower area the lowest (104).

RELATION OF SURVIVAL OF EGGS AND ALEVINS TO TIME OF SPAWNING OF ADULTS

The observed relation of fresh-water survival to the date by which 50 percent of the spawners entered Sashin Creek is shown in figure 2. The regres-

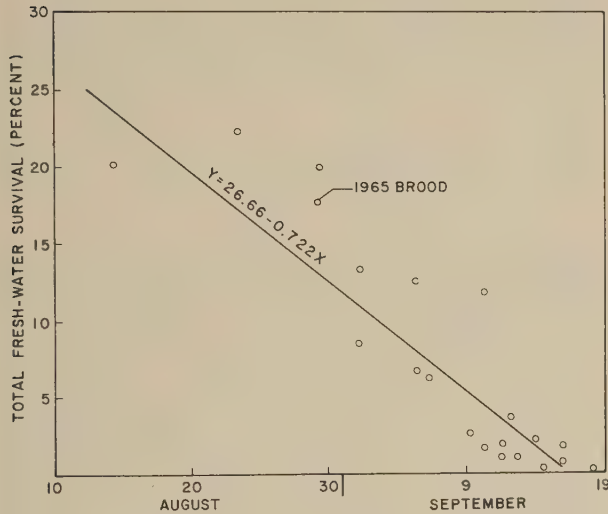


FIGURE 2.—Relation of fresh-water survival of pink salmon in Sashin Creek to date by which 50 percent of spawners entered the stream. The curve $Y = 26.66 - 0.722X$ was fitted by least squares, $X = 0$ corresponds to August 10. Relation of the 1965 brood year to the fitted regression is shown.

sion line in the figure is fitted to points for 20 brood years in the period 1940–64. Four years (1952, 1954, 1960, and 1962) were excluded from the regression because potential egg deposition was very meager (12,000 eggs or less) and one year (1964) because the adults were transplanted to the creek.

Fresh-water survival has exceeded that of the 1965 brood year in only three other brood years—1957, 1961, and 1963. In each year 50 percent of the spawners had entered the stream on or before August 26, the “index date” of stream entry for 1965. The date was August 22 in 1957 (22-percent survival); August 13 in 1961 (20-percent survival); and August 26 in 1963 (20-percent survival).

The predicted fresh-water survival of the 1965 brood year based on the regression line in figure 2 was 15 percent. The estimated survival based on the number of alevins collected with a hydraulic sampler (McNeil, 1964a) before the fry emerged from the streambed was 18 percent. An estimated 2,235,000 fry were produced. Although I could not compare this figure with a count of fry at the weir in the spring of 1966, survival estimated with the hydraulic sampler has agreed closely with survival estimated at the weir (table 9).

It is not entirely clear why fresh-water survival of pink salmon should be high in Sashin Creek when spawners enter early. Merrell (1962) hypothesized that embryos from eggs deposited late in the spawning season fail to develop sufficiently before the onset of cold weather and that embryos of retarded development are more sensitive to adverse effects of cold water than are more developed embryos. High mortality of pink salmon in streams tributary to the White and Barents Seas in 1960 was attributed to late spawning (Azbelev, Surkov, and Yakovenko, 1962).

Laboratory experiments indicate that exposure of salmon eggs to cold water soon after fertilization is detrimental, and this effect may partly explain why late spawning is less successful than early spawning. Eggs of sockeye salmon (*O. nerka*) held at an initial incubation temperature of 7° C. experienced higher mortality than eggs held at 10°, 13°, and 16° C. (Andrew and Geen, 1960), and early exposure of salmon eggs to temperatures of 1° and 2° C. can be lethal (Seymour, 1956; Combs and Burrows, 1957; Efimov, 1962). If incubation temperatures are high enough initially, subsequent reduction to near freezing is not always harmful, but the duration of initial exposure to warm water is important. Seymour (1956) incubated eggs of chinook salmon (*O. tshawytscha*) 2 and 3½ weeks in warm water before exposing them to cold water. He found that eggs reared 2 weeks in warm water had a high mortality when exposed to cold water, whereas eggs reared 3½ weeks in warm water had a low mortality. Additional studies would be required to determine the effect of water temperature on the survival of pink salmon eggs in Sashin Creek and whether warm water during spawning is generally necessary for high survival.

VARIATION AMONG STREAM AREAS IN DENSITY OF FRY

When pink salmon spawners are abundant in Sashin Creek, the entire spawning ground is used intensively; but the largest number of fry per square meter comes usually from the upper area. This fact was discovered first for the 1959 brood fry (Merrell, 1962), and I observed a similar difference in subsequent years when spawners were abundant. The numbers of fry per square meter in the three areas for 4 brood years were as follows (data for the 1959 brood from Merrell, 1962) :

Brood year	Lower area	Middle area	Upper area
1959.....	135	250	325
1961.....	225	605	600
1963.....	174	268	360
1965.....	104	197	228
Mean.....	160	330	378

Even though the upper area can potentially produce more fry per unit area than the lower or middle area, observations each year since 1958 show that spawners do not concentrate there. In 1965, 14,833 fish (both sexes) spawned at about equal density in the upper and middle areas and at somewhat lower density in the lower area (table 3). In 1964, when the number of spawners was only 2,193, they were concentrated in the lower area, and relatively few were in the upper area (Smedley and McNeil, 1966). In 1963, Sashin Creek had 16,757 spawners, and the number of females per square meter was 50 percent greater in the middle area than in the upper or lower area (McNeil, 1966). Only eight pink salmon spawned in 1962; no observations were made on their distribution. In 1961, 28,759 spawners were distributed fairly uniformly throughout the spawning ground (McNeil, Wells, and Brickell, 1964). Because an attempt was made to destroy the run in 1960, no observations were made on distribution of spawners that year. Data from Merrell (1962) indicated that in 1959, when 35,391 were present, the number of females per square meter in the middle area was at least twice that in the lower or upper. Spawners were scarce in 1958 (217), and they concentrated in the lower area (Merrell, 1962).

The distribution of spawners in Sashin Creek may depend somewhat on the time of spawning. Tagged females in 1963 (table 5 of McNeil, 1966) and 1965 (table 10) "shifted" downstream after the midpoint of spawning: early spawners tended to concentrate in the upper and middle areas and late spawners in the lower area.

TABLE 10.—*Expected and observed numbers of early and late spawning tagged female pink salmon in three study areas in Sashin Creek, 1965*

[Tagged spawners that first occupied the spawning ground by August 31 were designated as "early"; tagged spawners that occupied the spawning ground September 1 and later were designated as "late"]

Study area	Early spawners		Late spawners	
	Expected	Observed	Expected	Observed
	Number	Number	Number	Number
Upper.....	25	30	20	15
Middle.....	36	41	29	24
Lower.....	41	31	33	43
Total.....		102		82

$$\chi^2 (2 \text{ d.f.}) = 9.27 (P, 0.01).$$

In an earlier paper (McNeil, 1966) I attributed the downstream shift from the upper area in 1963 to turbulent water caused by heavy rainfall in the latter half of the period of spawning (4.5 cm. per day average from September 3 to 29, 1963); but in 1965, rainfall in September averaged less than 0.2 cm. per day, and the streamflow remained low throughout the latter half of the period of spawning—a condition opposite to 1963.

It now appears that late spawners are less inclined to occupy upstream spawning beds of Sashin Creek than are the early spawners, regardless of waterflow. My earlier interpretation of the cause of the downstream shift of the late spawners now appears to be incorrect.

RELATION OF WATER QUALITY TO SURVIVAL AND DEVELOPMENT OF EGGS AND ALEVINS

The concentration of dissolved oxygen in intra-gravel water in August and September 1965 helped confirm earlier conclusions (McNeil, 1966) that the environment is more favorable for eggs in the upper area than in the middle or lower area. Samples of intragravel water, collected from random points within each area August 16 and 31 and September 13 and 22, were analyzed for dissolved oxygen (table 11).

Dissolved oxygen concentrations of intragravel water were high in August but low in September, when a drought became severe. The low values in September were due partly to consumption of the dissolved oxygen in the stream water by decomposing salmon carcasses. Dead salmon are usually removed from Sashin Creek during freshets, but no freshets occurred in September 1965. The dissolved oxygen cannot be replenished without extensive exposure to the air. The upper area, which has a steep gradient and turbulent water, provided for more rapid replenishment of dissolved oxygen than the calm water in the lower area, which has a shallow gradient. Metabolites that are not freely exchanged with the atmosphere, such as ammoniacal nitrogen, also may have accumulated in the lower area.

TABLE 11.—*Dissolved oxygen content of intragravel water in three areas in Sashin Creek, 1965*¹

Study area and date	Water temperature	Dissolved oxygen concentration		Degree of saturation
		Mean	90-percent confidence limits of mean	
	° C.	Mg./l.	Mg./l.	Percent
Upper:				
August 16	12	9.7	±0.7	90
August 31	12	9.9	±.7	91
September 13	11	6.2	±.9	56
September 22	12	7.6	±.8	71
Middle:				
August 16	12	8.9	±.8	82
August 31	12	9.7	±.7	90
September 13	11	3.8	±.8	34
September 22	12	4.3	±.6	40
Lower:				
August 16	12	8.5	±1.1	78
August 31	2 12	—	—	—
September 13	11	2.3	±.3	20
September 22	12	2.9	±.6	27

¹ Methods of sampling were described by McNeil (1962).

² The August 31 samples were collected 1 day after a freshet; the data for the lower area are omitted because 60 percent of the standpipes in the area had been washed away.

I expected to find that the percentage of eggs alive at the end of spawning would be highest in the upper area and lowest in the lower area because of the progressively decreasing amounts of dissolved oxygen in intragravel water downstream. On September 29, 84 percent of total eggs were alive in the upper area; 86 percent in the middle area; and 60 percent in the lower area (table 5). Although the lowest survival of eggs was in the lower area, as anticipated, I was surprised to find survival of eggs in the middle area similar to that in the upper area. The percentages of live eggs did not change significantly in any

of the areas between September 29 and November 20 (table 5).

The development of embryos was somewhat retarded in the middle and lower areas. Laboratory experiments have demonstrated that oxygen privation during early development may retard growth and development of embryos without causing death (Silver, Warren, and Doudoroff, 1963; Shumway, Warren, and Doudoroff, 1964). When oxygen is deficient, it is usual for hatching to be delayed. This fact was confirmed in Sashin Creek in 1965 where the percentage of eggs hatching by November 20 was 77 percent in the upper area, 30 percent in the middle, and 11 percent in the lower.

The tendency of late spawners to concentrate in the lower area (table 10) may have contributed to the later hatching there, but it was not a factor in the middle area where the proportion of early and late spawners was the same as in the upper area.² Temperature apparently was not a factor either, because repeated measurements of the temperature of intragravel water failed to demonstrate differences among the three areas. I conclude, therefore, that hatching was delayed in the middle area because embryos had been exposed to low concentrations of dissolved oxygen in September. The late hatching in the lower area may have resulted from a combination of later time of egg deposition and exposure to low dissolved oxygen.

DISAPPEARANCE OF EGGS AND ALEVINS FROM SPAWNING BEDS

The disappearance of eggs and alevins of the 1965 brood was characterized by (1) disappearance of relatively few eggs from the upper and middle areas in summer during spawning, (2) disappearance of relatively large numbers from the upper and middle areas in autumn after spawning, and (3) disappearance of many eggs from all three areas in winter.

Fewer eggs disappeared during spawning in 1965 than in 1963 even though the densities of spawners were similar (table 12). In 1963, when the density was about 0.6 female per square meter, 22 percent of the potential egg deposition was esti-

² A chi-square comparison of the proportion of early and late spawners in the upper and middle areas (χ^2 , degree of freedom, =0.17) demonstrated that the proportion of early and late spawners was the same in these two areas.

mated to have disappeared during spawning in the upper area, 42 percent in the middle area, and 62 percent in the lower area. In 1965, at similar densities of spawners, much smaller percentages of the potential egg deposition disappeared during spawning: 7 percent in the upper area, 5 percent in the middle area, and 31 percent in the lower area.

The high percentage of eggs deposited in 1965 may have resulted from low streamflow in the period of spawning. Except for a freshet on August 30, which produced a discharge of 3 m.³ per second, streamflow remained relatively low (less than 1 m.³ per second) throughout the period of spawning. Streamflow did not increase until October 3 (after spawning had ended) when a second freshet produced a flow of 7 m.³ per second.

TABLE 12.—Percentage of potential egg deposition of pink salmon that disappeared from three areas in Sashin Creek during autumn and winter, 1963 and 1965 brood years

Area and season	Estimated portion of potential egg deposition disappearing	
	1963 brood	1965 brood
	Percent	Percent
Upper:		
Summer (during spawning).....	22	7
Autumn (after spawning).....	32	24
Winter.....	2	27
Middle:		
Summer (during spawning).....	42	5
Autumn (after spawning).....	0	26
Winter.....	1	30
Lower:		
Summer (during spawning).....	62	31
Autumn (after spawning).....	0	0
Winter.....	0	24

¹ Estimate pertains to the early two-thirds portion of the period of spawning. Other estimates for summer were at the end of spawning.

A relatively high percentage of the potential egg deposition (36 percent) disappeared from the upper area of Sashin Creek after spawning in autumn 1963, but few eggs and alevins disappeared in winter (table 12). Because the pattern of disappearance was dissimilar in the middle and lower areas in 1963, I postulated that scavengers or predators may have concentrated in the coarse bottom materials of the upper area to feed on eggs and alevins (McNeil, 1966). As I will show shortly, however, turbulent water during periods of high discharge in autumn may also have contributed to the disappearance of eggs from the upper area.

The rate of consumption of eggs and alevins by scavengers and predators is not known, but many species of invertebrates are known to inhabit

spawning beds where they may feed on eggs and alevins (Briggs, 1953; Ahnell, 1961; McDonald, 1960). Other investigators (McLarney, 1964, and Phillips and Claire, 1966) have found that sculpins (*Cottus* spp.) are capable of penetrating into streambeds and will feed on eggs and alevins where fine particles do not restrict their movements. The population of sculpins in Sashin Creek has been estimated to include 15,000 to 20,000 fish 5 cm. or longer total length (McLarney, 1964). According to McLarney (personal communication), this number of sculpins would be capable of consuming a significant portion (perhaps 25–50 percent) of the total number of eggs estimated to have disappeared in the autumn of 1963 (about 1 million) and the autumn of 1965 (about 2 million).

McLarney (personal communication) also found that many eggs deposited in coarse materials are near the surface of the streambed and are vulnerable to predation and to removal from the bed by water turbulence. He detected the presence of eggs near the surface of the bed by artificially creating water turbulence within a 0.2-m.² circular screen placed on the surface of the bed and collecting the eggs that were released from the streambed. About 150 points were tested in this manner in each of the three areas during spawning in 1965 (about 25 points per area on each of six dates). The number of eggs collected by McLarney per 0.2 m.² in the upper area was 3 times the number in the middle area and 14 times the number in the lower area. Thus, eggs were most susceptible to predation and to removal from the bed by turbulent water in the relatively coarse bed materials of the upper area and least susceptible in the relatively fine materials of the lower area. This result helps to explain why no eggs disappeared from the lower area in the autumns of 1963 and 1965 (table 12).

Other studies have shown that the portion of eggs and alevins that disappear from Sashin Creek spawning beds varies from winter to winter. The number of eggs and alevins did not decrease during the winters 1961–62 and 1963–64 (McNeil et al., 1964; McNeil, 1966); yet in the winter of 1965–66, an estimated 27 percent of potential egg deposition disappeared from spawning beds of Sashin Creek. Factors causing the disappearance of eggs and alevins in the winter of 1965–66 have not been identified.

SEASONAL VARIATION IN MORTALITY IN SPAWNING BEDS

The number of live pink salmon eggs of the 1965 brood declined from an estimated 12.7 million at the beginning of spawning in summer to 8.3 million at the end. Mortality caused further reductions to 6.5 million in autumn and to 2.2 million in winter.

It is instructive to compare mortality of the 1965 brood with that of the 1963 brood. For this comparison, I have calculated values of the mortality coefficient, M , for the entire stream rather than for the individual areas as given in table 8 of this paper and in table 11 of McNeil (1966). The values for M for brood years 1963 and 1965 for period 1 (summer), period 2 (autumn), and period 3 (winter) are as follows:

Brood year	Summer	Autumn	Winter
1963-----	0. 76	0. 11	0. 07
1965-----	. 31	. 15	. 26

Although the rate of mortality both years was highest during spawning, the difference between the two years was appreciable ($2\frac{1}{2}$ times). Mortality in autumn was similar for the two years, but the difference between the years was pronounced in winter ($3\frac{1}{2}$ times). Differences in mortality coefficients are suggestive of differences in the environment encountered by the two populations, because the number of spawners was similar each year (16,757 in 1963 and 14,833 in 1965). The unusual drought which prevailed throughout September 1965 could have produced increased survival during spawning from increased efficiency of egg deposition in spawning beds and decreased survival in autumn and winter from delayed mortality of embryos and alevins exposed to low concentrations of dissolved oxygen early in development.

SUMMARY

1. The area of streambed in Sashin Creek used by pink salmon for spawning is 13,629 m.² Observations on distribution of spawners and survival of embryos and alevins are made annually in 97 percent of the spawning ground which is di-

vided into upper (2,945 m.²), middle (4,067 m.²), and lower (6,072 m.²) areas.

2. Migration of 14,833 pink salmon spawners to Sashin Creek in 1965 was relatively early, and high fresh-water survival of their progeny (18 percent of potential egg deposition) resulted in the production of 2,235,000 fry. High survival was predicted at the time the parents entered the stream from a linear relation of survival of progeny and the date the parents entered the stream.

3. Although the density of spawners was relatively high and fairly uniform throughout the stream, densities of fry were considerably different in the upper, middle, and lower areas. The highest density of fry (228 per square meter) was in the upper area; the lowest (104 per square meter) was in the lower area. The relatively high density of fry in the upper area and low density in the lower area resembled the situation in three previous years (1959, 1961, and 1963) when the density of spawners in the three areas was also relatively high.

4. Spawners do not concentrate in the upper area despite the existence of a favorable environment for embryos and alevins. Failure to concentrate in that area is most pronounced when spawners are scarce, but the reasons for this behavior remain obscure.

5. Delayed hatching of eggs in the autumn of 1965 was attributed to low dissolved oxygen in intragravel water, which resulted from a drought throughout September. Detrimental effects of the drought on embryos were least pronounced in the upper area where concentrations of dissolved oxygen in intragravel water were highest.

6. Rates of disappearance of eggs and alevins from spawning beds in 1965-66 were low during spawning and high during winter in comparison with previous years. Low waterflow in September 1965 may have allowed a better than normal recruitment of eggs to spawning beds. The disappearance of large numbers of eggs and alevins in winter is unexplained.

7. The rate of mortality of the 1965 brood year was two times higher during spawning than in autumn. This situation is contrasted with the 1963 brood, whose rate of mortality was about 7 times higher during spawning than in autumn and about 11 times higher than in winter.

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PRELIMINARY ANALYSIS OF THE CATCH CURVE OF THE PACIFIC SARDINE, *Sardinops caerulea* Girard

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ABSTRACT

This is a report on a method of estimating age-dependent changes in rates of natural mortality and the age- and season-dependent changes in rates of availability of the Pacific sardine. It includes estimates of the virtual average catch curve and relative year class strengths and deviations of individual curves from these estimates. The calculations are carried out with each of three sets of data: total California catch, catch per unit of effort in central California, and catch per unit of effort in southern California.

The average catch curve allows an estimate to be made of the increase in the natural mortality rate during fully recruited ages. The deviations of individual curves are assumed to represent the annual changes in

rate of availability of each year class under a certain condition. The deviations of different age groups in the same years are compared to give a general idea of age-dependent change in the rate of availability in a year. Availability is also examined in regard to ocean temperatures preceding the fishing season.

A detailed model is proposed to estimate parameters relevant to the sardine population on the basis of the above examination as well as on the basis of earlier estimates of rates of natural mortality and availability. Consideration of the detailed model indicates the necessity for several sources of information to establish methods for predicting the sardine catch.

A fisherman's income depends on the size and behavior of stocks of fish entering his fishing grounds as well as on the efficiency of his gear. A fishery biologist must predict the size of the fish stocks available to the commercial fisheries. Taylor's² multiple regression equation, based on temperature and salinity in the year of spawning and on body length at the end of the first year of life, predicts the virtual stock size of a Pacific sardine year class. Availability of this fish, however, varies from season to season (Widrig, 1954), thus complicating the problem of prediction. To be useful to the fishermen, therefore, forecasts are needed for particular seasons and they must be based on yearly changes in availability in addition to year-class strength.

Widrig (1954) used relative rate of availability of the Pacific sardine to estimate population sizes and Yamanaka³ developed a method for estimating the absolute value of the rate. Both authors started from the formula:

$$Z = M - \log \{re^{-rQ} + (1-r)\} \quad (1)$$

¹ This manuscript was prepared during the author's visit at the Bureau of Commercial Fisheries Biological Laboratory, La Jolla, Calif., November 1959 to October 1960.

² Taylor, Clyde C. Some factors associated with year class size of the Pacific sardine. Bureau of Commercial Fisheries Biological Laboratory, La Jolla, Calif. (Manuscript).

Published May 1968.

where Z and M denote instantaneous coefficients of total and natural mortalities as defined by Holt, Gulland, Taylor, and Kurita (1959). Other symbols are defined as: f =amount of effort, Q =efficiency of unit effort, and r =rate of availability.

Widrig (1954) and Yamanaka³ assumed that the rates of natural mortality and availability are constant for four age groups (III- to VI-year-old fish). Introducing age-dependent changes in these rates into the calculations complicates the problem. Because the above authors did not do so, it is necessary to check the assumptions of equation (1) from another point of view.

In this paper I am interested in three matters. First I determine, through a simple examination of the catch data, if there is evidence of age-dependent changes in natural mortality and in availability. I also compare the various estimates of availability and their relation to an environmental factor, ocean temperature. Then I present a method to estimate the parameters on more probable assumptions resulting from these examinations.

GENERAL STATEMENT

In the first examination of the age data, I made

³ Yamanaka, Ichiro. Some notes on the natural mortality and availability of the California sardine. Nankai Regional Fisheries Research Laboratory, Kochi, Japan (Manuscript).

no attempt to estimate the absolute value of rate of availability, but rather I estimated the fluctuations in it as related to season and age. Strictly speaking, availability should be divided into two categories: (a) accessibility, the fish stock (in terms of numbers) accessible within the range of the fishermen and (b) vulnerability, which depends on factors involving gear efficiency. Measuring vulnerability in the commercial catch requires more than the examination of age composition and the amount of effort. I comment on this problem later. In the absence of information to separate availability into its components, their separate effects are disregarded here and included in the changes in availability and mortality.

Two basic assumptions are requisite for the first study of the relation of fluctuations to season and age: first, that the total mortality coefficient fluctuates randomly around a mean; and second, that the rate of availability fluctuates around a logarithmic mean. Even though no fishery may satisfy these assumptions, they may be accepted for a first approximation when age and year class are significant sources of variation in catch compared to the interaction that is a measure of total effects of changes in rates of mortality and availability as well as survey errors. In other words, changes in mortality and availability are regarded as less important in determining the catch than age and year-class strength when the latter two are significant sources of variations.

FORMULATIONS

Without exception the number of the i th year class caught in the year when they were j th age, C_{ij} , is expressed as:

$$C_{ij} = N_{i0} \cdot r_{ij} \cdot E_{ij} \cdot \prod_{a=0}^{j-1} S_{ij} = N'_{i0} \cdot r_{ij} \cdot E_{ij} \cdot \prod_{a=tp}^{j-1} S_{ia} \quad (2)$$

where: S_{ij} = annual rate of survival of the i th year class at j th age, E_{ij} = rate of exploitation for the available part of the i th year class at j th age, tp = youngest age in maturing spawning products, N_{i0} = initial stock size of the i th year class, N'_{i0} = stock size of the i th year class at the beginning of the year when they were tp year (s) old.

Under conditions assumed above, it holds that

$$\log C_j = \log N'_{i0} - \sum_{a=tp}^{j-1} Z_a + \log r_j + \log E_j \quad (3)$$

where, $\log C_j$ = logarithmic average of all catches of j th age fish over year classes, $\log N_0$ = logarithmic average of recruitment stock sizes over

year classes, Z_a = average mortality coefficient at a th age over year classes, $\log r_j$ = logarithmic average of availability rates at j th age over year classes, $\log E_j$ = logarithmic average of exploitation rates at j th age over year classes and

$$\log C_{j+1} = \log N'_0 - \sum_{a=tp}^j Z_a + \log r_{j+1} + \log E_{j+1} \quad (3')$$

and then

$$\log C_{j+1} - \log C_j = -Z_j + (\log r_{j+1} - \log r_j) + (\log E_{j+1} - \log E_j) \quad (4)$$

If j th age fish migrate with fish older by 1 year, formula (4) approaches $-Z_j$ for data available over a period of years, if there is no trend in the rates of exploitation and availability, or if the number of years is large. Thus, the logarithmic means of several ages of fish give a "standard virtual catch curve" for a given period under the above conditions. The standard curve becomes more reliable in estimates of $-Z_j$ as the period under consideration becomes longer and the catch curve of each year class becomes more stable.

Year-class means of $\log C_{ij}$, $\log C_i$, are

$$\log C_i = \log N'_{i0} - \sum_{a=tp}^{t_i} k_a Z_{ia} + \log r_i + \log E_i \quad (5)$$

where $k_a = (t_i - a + 1) / (t_i - t_p + 1)$, and t_i = the oldest age in question. The last two terms are the year-class means of the logarithms of rates of availability and exploitation, respectively.

These means may not give a good estimate of year-class strength in the sardine because its life span is too short to allow changes in rates of availability and exploitation to cancel each other. It may be regarded, however, as a measure of the mean available stock size of each year class when the year class is found to be a significant source of variation.

Since the logarithmic mean of catches is

$$\log C = \log N'_0 - \sum_{a=tp}^{t_i} k_a Z_a + \log r + \log E \quad (6)$$

we can construct an "expected catch," $E(\log C_{ij})$, when $Z_{ia} = Z_a$ is common for the entire year class and $r_{ia} = r_i$ and $E_{ia} = E_i$ are common for all the age groups of any year class.

$$\begin{aligned} E(\log C_{ij}) &= \log C_i + \log C_j - \log C \\ &= \log N'_{i0} - \left\{ \left(\sum_{a=tp}^{j-1} Z_a \right) \right. \\ &\quad \left. + \sum_{a=tp}^{j-1} k_a Z_{ia} - \sum_{a=tp}^{t_i} k_a Z_a \right\} \\ &\quad + (\log r_i + \log r_j - \log r) \\ &\quad + (\log E_i + \log E_j - \log E) \quad (7) \end{aligned}$$

Therefore,

$$\begin{aligned} \Delta_{ij} &= \log C_{ij} - E(\log C_{ij}) \\ &= - \left\{ \sum_{a=t_p}^{j-1} Z_{ia} - \left(\sum_{a=t_p}^{j-1} Z_a + \sum_{a=t_p}^{t_1} k_a Z_{ia} - \sum_{a=t_p}^{t_1} k_a Z_a \right) \right\} \\ &\quad + \{ \log r_{ij} - (\log r_i + \log r_j - \log r) \} + \{ \log E_{ij} \\ &\quad - (\log E_i + \log E_j - \log E) \} \quad (8) \end{aligned}$$

Among the variables in formula (8), we can determine combined effects of yearly changes in mortality coefficients and availability rate. Because $\sum_j \Delta_{ij} = 0$, the deviations of the same year class should be negatively correlated when the changes in rates of availability and exploitation are less important than change in mortality coefficients in determining the catch curves. On the other hand, significant positive correlation between deviations of any two age groups taken in the same seasons indicates that deviations in availability and exploitation are important.

A similar meaning attaches to any measure that is proportional to the available stock size, such as catch per unit of effort; here the change in rate of exploitation is disregarded. It should be noted that the deviations are affected by the year-class average of logarithms of availability and are not, then, a measure of relative availability on the same base.

TOTAL CALIFORNIA CATCH

Age composition of the California sardine has been reported for 26 seasons, 1932-33 through 1957-58 by Eckles (1954), Wolf (1961), Felin and Phillips (1948), Mosher, Felin, and Phillips (1949), Felin, Phillips, and Daugherty (1949), Felin, Daugherty, and Pinkas (1950, 1951), Felin, Anas, Daugherty, and Pinkas (1952), Felin, MacGregor, Daugherty, and Miller (1953, 1954, 1955), Felin, Wolf, Daugherty, and Miller (1958), Wolf, MacGregor, Daugherty, and Miller (1958), and Daugherty and Wolf (1960). When catch is plotted against age on a semilog scale for each year class, the catch curves are fairly smooth for fish older than age II of most year classes, but are very irregular for some year classes—especially those spawned in 1947 through 1949 (fig. 1). These irregular curves may be due to changes in availability and exploitation. The catch curves of some year classes indicate moderate irregularity. For instance, year classes 1930 through 1933 might have been highly available in the 1936-37 season.

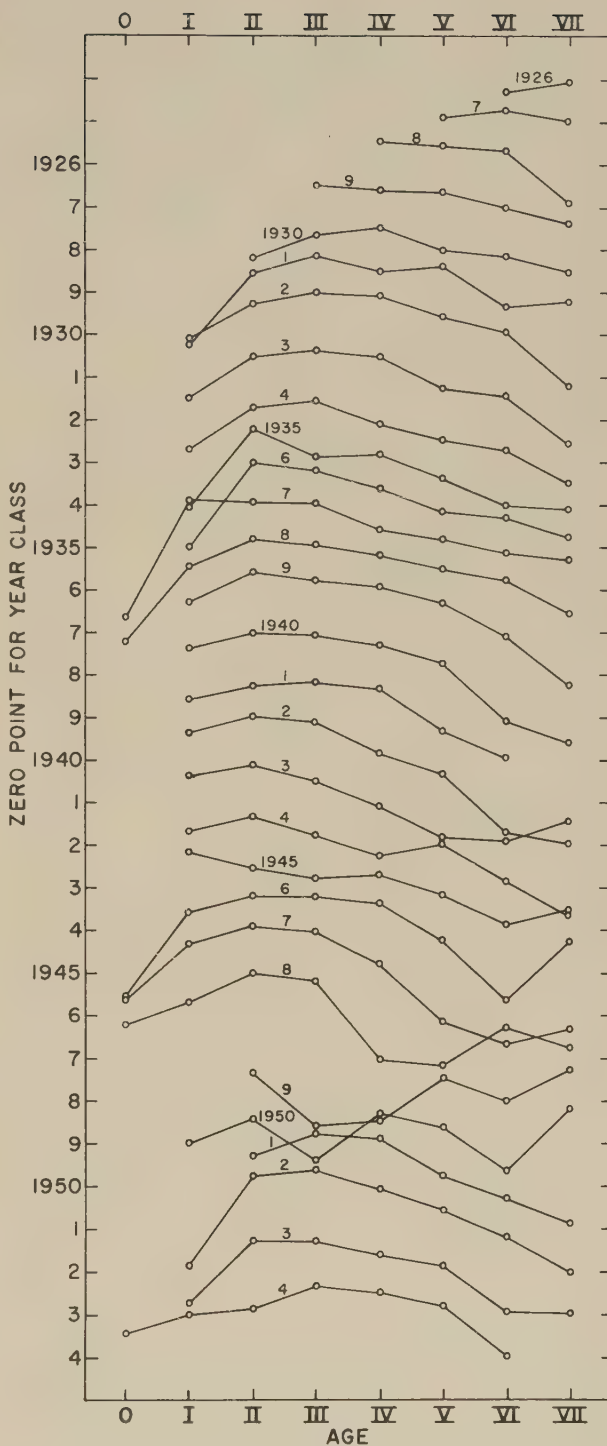


FIGURE 1.—Catch curves of Pacific sardine, year classes 1926 through 1954. Vertical scale equals log of millions of fish; distance between zero points for each year class equals 1.0 (i.e., 10,000,000 fish).

The age- and year-class mean of $\log C_{ij}$ for the 22 year classes from 1930 to 1951 are, nevertheless, regarded as sufficiently significant to give a reliable standard catch curve and estimates of year-class

strength of the available stocks. Analysis of variance of the means of logarithms of the total sardine catch in California for the year classes 1930 through 1951 gives the following:

Source of variation	Degrees of freedom	Mean square
Age.....	4	*6.1756
Year class.....	21	*1.3825
Residual.....	84	.2851

*Significant at a probability of less than 0.1 percent.

The average catches by age indicate that sardines are not fully recruited until age III (table 1). The increase in the mortality coefficient, even after age III, may be attributed partly to incomplete recruitment after this age and partly to an increase in natural mortality.

TABLE 1.—Mean sardine catch (ln), total mortality coefficients, and change in mortality by age for the year classes 1930–51 and 1930–44 in California

Age (j)	Mean catch (ln)		Mortality coefficient (Z_j)		$Z_{j+1} - Z_j$	
	1930–51	1930–44	1930–51	1930–44	1930–51	1930–44
	Millions of fish	Millions of fish				
II.....	310.0	646.7				
III.....	340.9	579.9	–0.09	0.11	0.72	0.60
IV.....	176.5	284.0	.63	.71	.32	.28
V.....	65.1	104.9	.95	1.00	.24	.23
VI.....	18.8	30.6	1.19	1.23		

Because of incomplete records, the expected catches of eight year classes, 1926–29 and 1951–57, are constructed through their mean catches and a standard catch curve, so that $\sum_j \Delta_{ij}$ reduced to zero. When these additional classes are included, the deviations of logarithmic catches of any two age groups in the same season are positively correlated with each other, where the effects of environment and fishing intensity might be expected to be common for all the age groups. The correlation coefficient is higher for combinations of adjacent age groups (fig. 2). On the other hand, correlation coefficients between deviations in two ages from the same year classes range from –0.690 to 0.307. This variability indicates that change in survival rate is less important than change in availability and exploitation.

From these observations in regard to assumptions given in the last two paragraphs of the

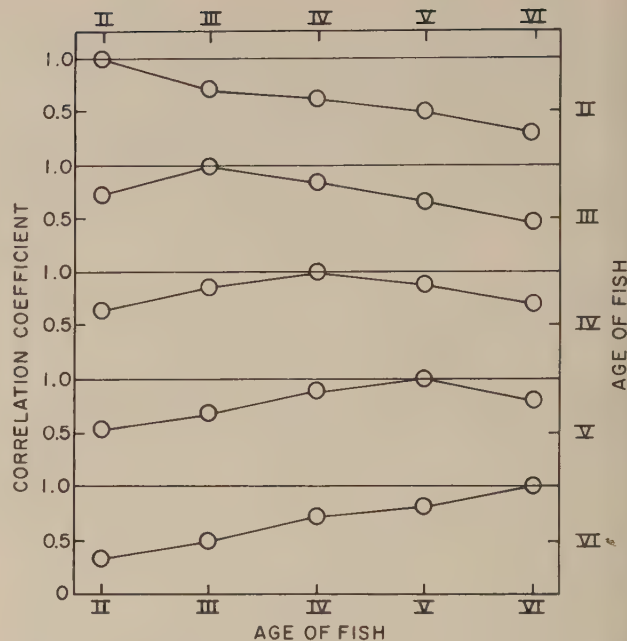


FIGURE 2.—Correlation coefficients between index of virtual availability of two age groups, based on the total catch in California, 1932–33 through 1957–58 seasons.

preceding section (on formulations), it may be assumed that the year-class-dependent change in total mortality coefficients is smaller than the seasonal changes in both availability and exploitation and that the migratory pattern differs from age to age but is similar for adjacent ages. The multiple correlation of deviations of age groups III to V in the same season was calculated to be as high as 0.815. These three age groups furnished the greater part of the period under discussion.

It is well known that the migratory pattern of the Japanese sardine and its fishing grounds are affected by changes in oceanographic conditions (Sako, 1939; Shimomura, 1954). Because sufficient information about the environment of the fishing grounds in California waters was lacking, I correlated the temperature anomaly at the pier of the Scripps Institution of Oceanography for July through September (just before the fishing season) with annual mean deviations in the catch of the three major age groups for 26 seasons (fig. 3). The correlation coefficient was 0.599, slightly over the 1-percent level of significance.

Clark and Daugherty (1950) reported the catch per unit of effort and total effort of the purse seiners in California waters as well as at each of the three major ports, San Francisco, Monterey, and San Pedro, for the seasons 1932–33 through 1948–49. To eliminate the effects of improvement

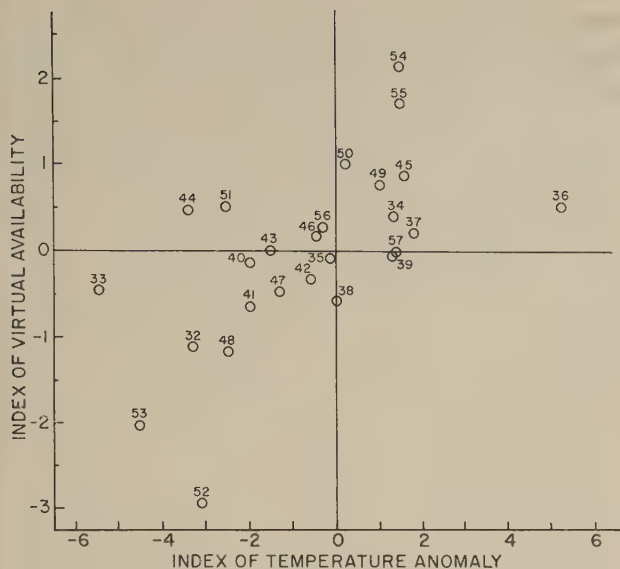


FIGURE 3.—Relation between temperature anomaly at pier of the Scripps Institution of Oceanography and virtual availability of sardines in California, 1932-33 through 1957-58 seasons. Numerals denote the fishing season, e.g., 32 indicates the season of 1932-33.

in the efficiency of individual boats, they adjusted the catch per unit of effort using as base year the 1932-33 season at each port. The same authors (1952) reported the data for the 1949-50 and 1950-51 seasons in all California waters, as well as at Monterey and San Pedro, and Clark (1956) published the data for the four seasons 1951-52 through 1954-55 in southern California. In the latter two works the authors chose the 1941-42 season as the new base year (Clark and Daugherty, 1950) to fit recent developments in the fishery.

Because fishing effort should be expressed on the same base year, I converted the catch per unit of effort in the whole fishing season to the value based on that of the 1941-42 season. Since the fishing grounds off California are divided into two regions of almost equal area, the north off San Francisco and Monterey and the south off San Pedro (Widrig, 1954), the total effective effort is calculated by dividing the total California catch by the sum of catches per unit effort in the two regions. The deviations of catch showed a significant multiple correlation coefficient of 0.594 with the temperature anomaly and the amount of fishing effort. Partial correlation coefficients were 0.293 for fishing effort and 0.585 for temperature anomalies.

CATCH PER UNIT OF EFFORT

Because fishing effort appeared to show a positive correlation with the deviation of catch from the expected value, I repeated the above calculations for total catch, using the catch per unit of effort. Present evidence indicates that the stock exploited in the waters off central California is mainly composed of fish spawned in the waters off southern California (northern subpopulation), whereas the stock in southern California includes fish spawned off central Baja California (southern subpopulation) as well as fish from the northern subpopulation (Felin, 1954; Marr, 1960). The effort data are not given after the 1951-52 season for central California where the fishery practically disappeared by 1954. Catch per unit of effort at San Francisco, Monterey, and San Pedro indicates that the available stocks off the two northern ports are correlated with a significant coefficient of 0.810 but that the stock off San Pedro is not correlated with either San Francisco (0.314) or Monterey (0.398) during the 19 seasons from 1932-33 to 1950-51. This lack of correlation may be attributed to differences in the subpopulation supporting the fisheries. It is also possible that the northern subpopulation, having migrated to central California, left only a minor portion of the stock in southern California or that major age groups differed between these regions.

Since it is desirable to forecast regional catches, the following discussion is based on data by region. In the northern waters the catch curves for ages II to VI, based on catch per unit of effort, were obtained for the 1930-44 year classes. The curves were fairly regular for most of the year classes, except the last. The following table shows that age and year class are significant sources of variation of logarithmic catch, as was true for total catch:

Source of variation	Degree of freedom	Mean square
Age.....	4	*4.4487
Year class.....	14	*1.2050
Residual.....	56	.1596

*Significant at a probability of less than 0.1 percent.

The following tabulation of the standard catch curve based on logarithmic means of the catch per unit of effort in central California for the year classes 1930-44 shows that there is less change in

mortality rate with age than was found for total catch (table 1):

Age (j)	Mean catch (thousands of fish)	Mortality coefficient (Z_j)
II.....	656.6	
III.....	592.5	0.10
IV.....	264.7	.81
V.....	102.5	.95
VI.....	33.7	1.11

The deviations from the expected catch for some year classes did not always indicate significant negative correlation; the coefficients range between -0.661 and 0.478. On the other hand, the deviations in the same season were always positively correlated; the coefficients vary between 0.280 and 0.850. It is again found that the closer the ages, the higher the correlation coefficients. The multiple correlation coefficient for the three major age groups is 0.877.

In the southern California catch, the curves were irregular for the year classes that occurred after 1947. The following analysis of variance of the means of logarithms of the catch per unit of effort in southern California for the year classes 1930-48 shows that age and year class are significant sources of variation:

Source of variation	Degrees of freedom	Mean square
Age.....	4	*1.6133
Year class.....	18	*2.0954
Residual.....	72	.1244

*Significant at a probability of less than 0.1 percent.

The standard catch curve is fairly smooth after age III; age-dependent changes in mortality are minor. The four year classes that were produced in 1945-48, however, may differ in survival rate as well as in stock size (table 2). The correlation coefficient between deviations of the same year class fluctuates broadly between -0.495 and 0.138. The correlations between deviations in the same season are always positive, 0.223 to 0.890, and are higher for two adjacent age groups; the multiple correlation coefficient for age groups III to V was as high as 0.910.

The mean deviations for age groups III through V in central and southern California fluctuate similarly; the correlation coefficient between them was 0.810. Compared with the different regional fluctuations in catch per unit of effort of all the

TABLE 2.—Mean sardine catch ($\ln$), total mortality coefficients, and change in mortality by age for the year classes 1930-48 and 1930-44 in southern California

Age (j)	Mean catch ($\ln$)		Mortality coefficient (Z_j)		$Z_{j+1}-Z_j$	
	1930-48	1930-44	1930-48	1930-44	1930-48	1930-44
	Millions of fish	Millions of fish				
II.....	907.6	888.5				
III.....	701.9	680.2	0.26	0.27		
IV.....	251.1	283.6	1.03	.87	0.77	0.61
V.....	71.1	85.2	1.26	1.20	.24	.33
VI.....	18.8	14.3	1.33	1.49	.07	.29

age groups, this similarity may suggest that some younger and older age groups than those in question showed different changes in availability between these two regions.

The temperature anomaly at Scripps pier does not correlate well with the deviations in catch, but is slightly higher with those in central California (0.560) than with those in southern California (0.495).

DYNAMICS OF THE PACIFIC SARDINE FISHERY

This discussion deals with the age-dependent changes in rates of natural mortality and availability derived from information obtained thus far. A detailed model is presented for estimating the parameters inherent in the population dynamics of the Pacific sardine.

All three sets of data analyzed above indicate three characters of catch curves of the sardine: (a) the increase of the virtual total mortality coefficient with age; (b) the close relation between virtual indices of availability of two adjacent age groups; and (c) the dependence of the availability on temperature in the months just before the fishing season. To examine the reliability of these findings, similar analyses are repeated with estimates of these parameters as presented by Widrig (1954) and Yamanaka (footnote 3).

Previous authors assumed that the natural mortality coefficient was constant over the four age groups III through VI. In Widrig's study (1954) three appropriate values of the coefficients were assumed, and the rate of availability in a season was shown in relative rate to that of the 1936-37 season for each of these assumed coefficients. Yamanaka (footnote 3) assumed that the

natural mortality coefficient fluctuated around a mean and that the rate of availability fluctuated around a logarithmic mean for the 23 seasons from 1932-33 to 1954-55. Because the level of availability changed between the early and later years of the investigation, he divided the period into two parts; one from 1932-33 to 1945-46, and the other from 1945-46 to 1954-55. The present report examines only his final estimates based on the divided data. Because these authors first estimated the rate of availability in logarithms, my analysis of the rate is usually made with logarithmic rather than actual values.

As estimated by Yamanaka (footnote 3), the increase in virtual total mortality coefficients with age is comparable to decrease in availability of older fish. As expected from his assumption, availability should decrease with age if total mortality increases. Therefore, I conclude that the virtual coefficient of total mortality of the Pacific sardine increased with age for the period investigated.

The age-dependent change in the virtual coefficient of total mortality may be partly attributed to incomplete recruitment⁴ in addition to a real change in natural mortality, insofar as it is estimated from the age composition of the commercial catch. Although no conclusive evidence is obtained, it seems to me that the increase in natural mortality with age is real rather than caused by incomplete recruitment for the fish at and older than the three ages discussed, since the fishery has exploited fish as young as age I and sometimes age zero. If this increase in natural mortality with age is real, the natural mortality coefficient of these fish is considered to increase linearly with age (table 1). A linear increase of the coefficient with age was postulated by Beverton and Holt (1957, pp. 69-71) for three species: two herrings, *Clupea harengus harengus* and *C. harengus pallasi*, investigated by Hodgson (1932) and Tester (unpublished, cited by Ricker, 1948) and the whitefish, *Coregonus clupeaformis*, of Lake Opeongo studied by Ricker (1949). A linear increase with age may not always hold, however, as was shown for the same species, or ecologically related ones, surveyed on other occasions: namely the whitefish of Shakespeare Island Lake, the

sauger, *Stizostedion canadense*, of Lake Opeongo (Ricker, 1949), and the herring, *C. harengus pallasi* (Tester, 1955).

It is noteworthy that total mortality coefficients are higher in southern California than in central California—also the increments, which average about 0.30 in southern California but 0.15 in central California, as previously shown. This difference is partly attributed to differential distribution of the fish by age; older fish migrate farther north. It should be noted, however, that Yamanaka (footnote 3) estimated the natural mortality coefficient of the sardines to be higher in the more recent years, when the southern subpopulation predominated, than in earlier years for the entire range of the fishery in California. Thus, both his and my results agree that the mortality rate is higher in the southern subpopulation than in the northern one.

It has been shown thus far that the rate of availability differed between age groups exploited in the same fishing season but that it was close for two adjacent age groups. A comparable result is obtained from the analysis of the availability rates as estimated by Yamanaka (footnote 3). As to the age-dependent change in availability, it has already been suggested that some species of fish school together by size or by age, including, among others, the herring, *C. harengus* (Hjort, 1926, p. 8); the sardine, *Sardinops melanosticta* (Yamanaka, 1955, p. 51); the anchovies, *Engraulis mordax* (Miller, 1955, p. 30), and *Cetengraulis mysticetus* (Howard and Landa, 1958, p. 394); the yellowfin tuna, *Thunnus albacares* (Schaefer, 1948, p. 199); and the skipjack tuna, *Katsuwonus pelamis* (Brock, 1954, p. 99).

As an approach to predicting catch, the temperature data at Scripps pier just before the fishing season were regarded as having been correlated with the preliminary estimates of availability. The correlation coefficients between temperatures and the logarithms of each series of estimates by Widrig (1954), based on assumed values of the natural mortality coefficients of 0, 0.2, and 0.4, are 0.256, 0.305, and 0.300, respectively. Since Yamanaka (footnote 3) estimated the natural mortality coefficient to be 0.35 for all the seasons, or 0.25 for 1932-33 through 1945-46 and 0.65 for 1945-46 through 1954-55, the most probable rate of Widrig's estimates of availability, based on the assumed natural mortality coefficient of 0.4, is best correlated with temperature. In Yamanaka's estimates, the correlation coefficient with

⁴ Age of complete recruitment of a partially available population is defined as the age at which all the fish are potentially "catchable" by the fishery even if, actually, some of them do not always enter the fishing ground. When rates of availability are estimated for all the age groups appearing in the catch, the age of complete recruitment is determined by comparison of the average rate for each age.

temperature is 0.686—higher than that calculated by me or by Widrig (1954).

The correlation coefficient based on the rate of availability is 0.757 and, thus, higher than that based on the logarithmic values.

Summarizing these examinations of the age composition of the sardine catch by Widrig (1954), Yamanaka (footnote 3) and the present study, I may be able to assume the following characteristics of the available sardine stocks:

a. The natural mortality differs by age and by subpopulation and probably by year class; therefore, I recommend that the rate be estimated for each age group with the data taken in the shortest period of years for which the analysis can be made and for each fishing ground in which the stock is more homogeneous.

b. The availability also differs by age of the fish. It is indicated, however, that the rates of two successive age groups are similar. This fact also indicates that the parameters should be estimated for each age group separately.

c. Availability seems to be correlated with temperature. This possibility should be studied in relation to temporal and areal patterns of the environment, as well as the general levels of availability. For instance, Craig (1960) demonstrated that the herring catch was related to increase in temperature and strength and direction of winds in early summer, even though the catch was not highly correlated with each of these factors. Factors such as these, regarded important in Japan, include temperature distribution, intensity of cold water masses (upwelling), and current strength and direction (Shimomura, 1954).

A more detailed model is presented on the basis of age specific mortality and availability characteristics. Because rates of availability of two adjacent age groups in any year may be assumed to be almost the same, the virtual survival rate, S'_{at} , obtained from age and catch data is expressed as:

$$S'_{at} = \exp(Z'_{at}) = (N_{a+1 \cdot t+1}) / (N_{at} r_{at}) \\ = \{r_{at} e^{-f_t Q_{at}} + (1 - r_{at})\} e^{M_{at} r_{a+1 \cdot t+1} / r_{at}} \quad (9)$$

then

$$Z'_{at} = M_{at} - \log \{r_{at} e^{-f_t Q_{at}} + (1 - r_{at})\} \\ + (\log r_{at} - \log r_{a+1 \cdot t+1}) \quad (9')$$

where a and t denote age of fish and season,

respectively. It is assumed that r_{at} and Q_{at} are equal to $r_{a \cdot t+1}$ and $Q_{a \cdot t+1}$ respectively.

The mean of virtual mortality coefficients for n seasons is the sum of means of the first and second terms, and $(\log r_{a \cdot 1} - \log r_{a \cdot n+1})/n$. Then, if Q remains constant for a long period of years so that the last term diminishes to zero, the means of the parameters including Q , M , and r are estimated as shown by Yamanaka (footnote 3). The value of Q , however, should be regarded as variable during rather short periods of years, partly depending on gear improvement, such as the several gear improvements in the sardine fishery in California. In addition, Q may vary because of biological and economic reasons even if the same type of fishing gear is used. The major factors relating to this quantity may be classified in the following three groups:

a. The first and most essential factor affecting Q depends on such variables as fish size, gear type, and speed of hauling. This factor and the mechanical selectivity discussed below, defined as q in the following discussion, determined the efficiency of a fishery for a particular size of fish distributed in a certain way.

b. The second factor, selectivity, is related to both the fish and the fishery. Two general categories of selectivity should be distinguished. The first is a mechanical selectivity, such as the size and number of fish retained by the gear, and is determined by the relation between sizes of mesh or hook and fish; the second is an economic selectivity, controlled by market performance by size or species. The former type of selectivity is included in the first category (a above) of factors controlling Q . The mean of the latter selectivity factor is included in the rates of natural mortality. The deviation from mean is included in availability.

c. The third factor, volume of the water in which the available part of the stock is distributed, also causes change in Q even though the rate of availability is constant. The same gear should be more effective or the same fishermen should locate the schools more readily when the fish are distributed in smaller volumes of water than in larger ones. Changes in patchiness and depth of distribution may not be as important as the size of the waters when the discussion concerns a whole season during which total effects may be nearly constant. Since sardines may remain in a particular stratum, the volume of water may be approximated by the area of fishing ground, A , that is

measured by location of the hauls or isothermal contours.

The first approach regards the value of Q as q/A .

Since catch per unit of effort is related to the mean density of the fish stock in the fishing ground, as well as to the efficiency of individual gear, this quantity should be adjusted by an appropriate measure (such as area of fishing ground) to yield the relative stock size and the virtual mortality coefficient (Gulland, 1955; Beverton and Holt, 1957). Watt (1956, p. 629) pointed out that the catch per unit of effort, obtained by dividing the total catch by total effort in a season, is not realistic when availability changes within the season. He, therefore, compared the stock sizes in 2 years by the catch per unit of effort in a particular month.

If a fishery is operated in several localities, there is no reason to believe that rate of availability (accessibility and vulnerability) is common for the total range of the fishery. Each locality should be studied, especially if the stocks in different areas are composed of different subpopulations.

Such studies require that the calculations be carried on for shorter periods and over smaller areas. Because the mean of the last term of equation (9) does not reduce to zero for such a situation, we have to assume the following:

a. M and q fluctuate around their means at random, and their variances are so small that these quantities may be regarded as constant.

b. There is a mean of r that gives a mean of the second term for any given set of q , f , and A .

c. The ratio of availabilities in 2 adjacent years fluctuates around a logarithmic mean at random.

d. The availability and gear efficiency are common for two adjacent age groups.

On the basis of these assumptions, the virtual mortality coefficient of a certain age group of fish during the t th season, Z'_t , in an area is

$$Z'_t = M_t - \log \{ r_t \cdot \exp (-f_t q_t / A_t) + (1 - r_t) \} \\ + (\log r_t - \log r_{t-1}) \quad (10)$$

and the mean of the virtual mortality coefficients of the age group, Z' , is

$$Z' = M - \log \{ \bar{r} \exp (-f \bar{q} / A) + (1 - \bar{r}) \} + d \quad (11)$$

where $\bar{r}$ and $\bar{q}$ are estimated averages of r and q in the age group, which give the mean of the second term in the formula (10) for a given set of f and A , and $d = \log (r_1 / r_0) / m - 1$.

The parameters, M , $\bar{q}$, $\bar{r}$, and d , may be estimated by the least-squares method if appropriate data which were taken in at least 6 successive years and a suitable computer are available to make the calculations.

Putting $a_t = \exp (-f_t \bar{q} / A_t)$, and $b_t = \log \bar{r} a_t + (1 - \bar{r}) + d$, the expected virtual mortality coefficient, $E(Z'_t)$, equals $M - b_t$. The differences between observed and expected mortality coefficients, Δ 's, are:

$$\Delta_1 = \log \{ a_1 r_1 + (1 - r_1) \} + (\log r_1 - \log r_2) - b_1,$$

$$\Delta_2 = \log \{ a_2 r_2 + (1 - r_2) \} - (\log r_2 - \log r_3) - b_2,$$

$$\cdot \quad \cdot \quad \cdot$$

$$\Delta_5 = \log \{ a_5 r_5 + (1 - r_5) \} - (\log r_5 - \log r_1 + 5d) - b_5 \quad (12)$$

These equations give the rates of availability for these 5 years. Repeating this procedure for each successive 6-year period, we may obtain the running averages of the parameters on which a more advanced discussion can be made. When A is not accurately measured, the calculation of availability, based on the constant $Q = q/A$, may give some clues for estimating vulnerability. When fish show differential distribution by age, the mortality rate in the entire population may be estimated from the summation of the stock size of each age group in each locality. Before calculation, division of the area should be reexamined, such as by areal variation in fishing season and relative size of subpopulations (perhaps by scale characters as well as serological research).

Finally, it should be noted that this type of analysis does not provide absolute values of availability for a whole population. Estimates may differ from each other for availability of an age group in a season by six different series. If relative values of the estimated rates for successive seasons are comparable for all of the six series, however, the absolute rate may be surmised from information on the distribution of stocks and independent from fisheries, such as an egg census. As a matter of fact, estimates of availability rates in this type of analysis could be compared with geographic distributions of egg stocks. This comparison is based on the fact that the distribution of the parent stock of the Pacific sardine was represented by egg distribution for the 5 years

1952-56 (Ahlstrom, 1959, p. 204). Furthermore, a coincidence of distributions of parent stocks and their eggs was detected in the related species, *Sardinops melanosticta*, inhabiting the waters adjacent to Japan (Nakai, 1960, p. 821).

SUMMARY

The rate of natural mortality of the Pacific sardine seems to be higher in the older fish than in the younger ones and higher in the southern subpopulation than in the northern one. For this reason it is indicated that natural mortality should be estimated for the subpopulations by age from the catch data of two adjacent age groups.

Availability was found to differ by age as well as by season. High correlations were obtained between the rates of two adjacent age groups exploited in the same fishing season; therefore, this rate also should be estimated by examination of two adjacent age groups.

The data suggest that availability was positively correlated with water temperatures in July to September, immediately preceding the fishing season.

In addition to the above factors, others such as efficiency of gear and area of fishing grounds may affect the catch curves. The most promising procedures may be the comparisons of the total mortality coefficients, number of boats, and area of fishing grounds during the shortest time periods. Consideration of these facts indicates that running averages for six seasons should be computed for these factors.

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DIEL MOVEMENT AND VERTICAL DISTRIBUTION OF JUVENILE ANADROMOUS FISH IN TURBINE INTAKES

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ABSTRACT

The behavior of fingerling salmonids was measured in turbine intakes of The Dalles and McNary Dams on the Columbia River to aid in developing methods for reducing fish mortality in Kaplan turbines. At The Dalles Dam, diel movement and vertical distribution were sampled at both ends and at the middle of the section of the powerhouse that housed turbines 1 through 12. At McNary Dam, vertical distribution was sampled in intake 12-C, located near the middle of the River channel.

Comparisons of day-night occurrence at The Dalles Dam showed that most chinook salmon (*Oncorhynchus tshawytscha*), steelhead trout (*Salmo gairdneri*), and ammocoetes of the Pacific lamprey (*Lampetra tridentata*) were caught at night (7 p.m. to 7 a.m.). Vertical distribution studies at McNary and The Dalles Dams included catches of sockeye salmon (*O. nerka*) in addition to the above species. Salmonids were taken at

all depths, but most were in the upper 30 percent of water in the intakes (within 4.6 m. of the ceiling). Ammocoetes at The Dalles Dam (no data for McNary Dam) were concentrated near the center and bottom of the intakes; very few were near the ceiling.

To increase survival of fish by manipulating turbine loads during a 24-hour operational period appears feasible. During darkness when fish movements through turbines increase and power demands decrease, the reduction in turbine loads improves the flexibility for adjusting turbine loads to increase fish survival.

The concentration of fingerling salmonids near intake ceilings probably causes most of the fish to pass the turbine runner at or near the hub; therefore, methods for eliminating lethal factors at the runner should be applied first at the hub. In addition, use of deflection and bypass techniques near intake ceilings would be advantageous because the concentration of fish is greatest there.

The behavior of fingerling salmonids in turbine intakes, including their time of passage and distribution in the water mass, can profoundly influence development of efficient and economical methods for reducing fish mortality in turbines. The need for fish protection at dams is becoming particularly acute in the Columbia Basin because the progeny of upriver stocks of salmonids soon will be forced to pass through the turbines of 8 to 10 dams to reach the sea.

At present, normal spring flows are divided about equally between spillways and turbines; numbers of young fish migrating downstream presumably pass through the spillways and the turbines in proportion to the water passed by each. Studies at McNary and Big Cliff Dams under normal operating conditions (wicket gates opened

75–80 percent) have shown that mortality of young salmon in Kaplan turbines is about 11 percent, whereas mortality in the spillway is comparatively light—2 percent (State of Washington Department of Fisheries;¹ Schoeneman, Pressey, and Junge, 1961). Similar mortality is assumed to occur at other dams with comparable turbine designs and operational features.

Unless solutions are found, the total mortality will increase in the future. When the Corps of Engineers' Projects are completed, almost all water in the Columbia Basin's flow regime eventually will pass through turbines, eliminating the relatively safe passageway now provided by water

¹ State of Washington Department of Fisheries. Research relating to mortality of downstream migrant salmon passing McNary and Big Cliff Dams. Progr. Rep. Fish. Eng. Res. Program, 1960, N. Pac. Div., U.S. Army Corps Eng., pp. 122–126.

flowing over the spillways. Because of the imminent danger to future runs, the Bureau of Commercial Fisheries has a research program under way to develop methods for protecting fingerlings as they pass through turbines.

From the outset of this program, knowledge of the behavior of fish immediately upstream of turbines was required. Information on diel movement was essential for obtaining more precise measures of total mortality and for estimating the feasibility of different methods for protecting fish. Research at Big Cliff Dam by the State of Washington Department of Fisheries (footnote 1) showed that mortality at two turbine loads (40 versus 80 percent wicket gate openings) differed significantly. Because turbine loads fluctuate daily, it was obvious that mortalities also might vary daily. The estimation of average daily mortality required knowledge of (1) mortality for a wide range of turbine loads, (2) daily fluctuations of turbine loads, and (3) daily variation of fish movement through turbines. If the relation of these three factors were better understood, perhaps mortality

could be minimized by manipulation of turbine loads when most of the migrants are passing downstream at damsites.

Another facet of fish behavior, important to the development of protective methods, is the route used by most of the fish. Studies of models showed that flows through turbine intakes and associated scroll cases of dams such as McNary were well ordered; e.g., flows near intake ceilings pass by the top of the wicket gates, and flows near intake floors pass by the bottom of the wicket gates. Because the turbine blades lie only a few meters farther downstream, it is probable that distribution of flows at the blades corresponds with distribution of flows at the wicket gates; i.e., flows from the top of the wicket gates pass the blades at the hub, and flows from the bottom of the wicket gates pass the blades at their tips.² Thus, the distribution of fish at the turbine blades might be deduced with some degree of accuracy from the distribution of fish in the intakes. When fish distribution is known, meth-

² Personal communication. Johnson, G. Dugan, Allis-Chalmers Manufacturing Co., York, Pa.



FIGURE 1.—Location of present and future low-head dams on main stem, Columbia and Snake Rivers.

ods for eliminating lethal agents at the turbine blades can be applied at the specific area through which most of the fish pass. Knowledge of the extent of fish concentrations also can aid in determining the feasibility of guiding them into safe bypasses.

Information is available on diel movement and distribution of fingerling salmonids at several points in the river system. Mains and Smith³ studied timing and distribution of fingerling movement in river channels; Gauley, Anas, and Schlotterbeck (1958) investigated diel movement in special bypasses at Bonneville Dam. Because the physical environment in these studies differed markedly from that in turbines and associated water passages, the data could not be applied to turbine areas with complete confidence. Additional studies accordingly were proposed.

This paper reports on experiments at two dams on the Columbia River to acquire data on timing and distribution of fingerling salmonids entering turbine intakes. In 1960, diel movement and vertical distribution of fingerling salmonids were investigated at The Dalles Dam; data on lamprey ammocoetes also were obtained. In 1961, the vertical distribution of fingerlings was studied at McNary Dam.

RESEARCH AREAS

The Dalles and McNary Dams, operated by the U.S. Army Corps of Engineers, are hydroelectric projects on the Columbia River (fig. 1) with maximum heads of 27.0 and 27.5 m., respectively. Designs and dimensions of low-head dams on the Columbia River are similar, but the powerhouses are located parallel (The Dalles) or at a right angle (McNary) to the course of the River (fig. 2).

At the times of these experiments, in 1960 and 1961, The Dalles Dam had 12 operative turbines and McNary had 14. Turbines of both Dams are equipped with three intakes—A, B, and C. Each intake has a gatewell, or vertical shaft, which extends from an opening in the ceiling of the intake to the forebay deck. Figure 3 is a cross section of an intake at The Dalles Dam, showing the gatewell and other features. The turbines and turbine intakes of McNary Dam have a similar design.

³ Mains, J. E., and J. M. Smith. Determination of normal stream distribution, size, time and current preferences of downstream migrating salmon and steelhead trout in the Columbia and Snake Rivers. Progr. Rep. Fish. Eng. Res. Program, 1956. North Pacific Division, U.S. Army Corps of Engineers, pp. 14–26.

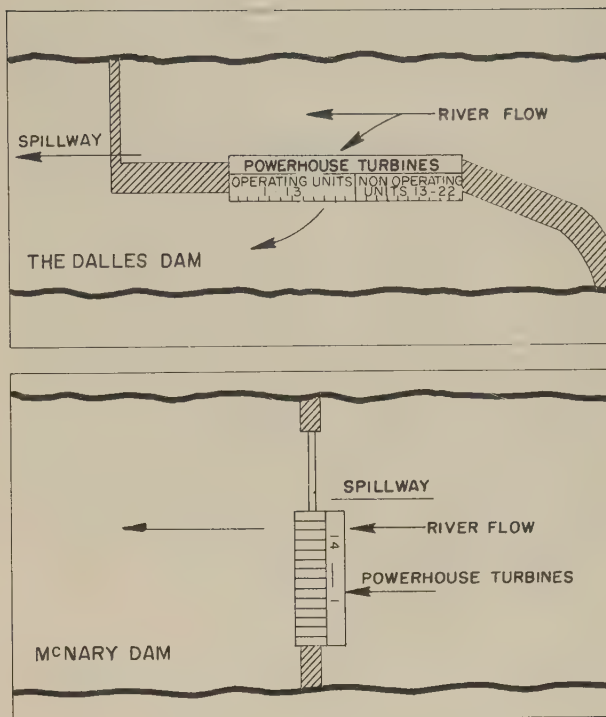


FIGURE 2.—Comparison of The Dalles and McNary Dams. The orientation of the powerhouse of The Dalles Dam, nearly parallel to the course of the River, causes water to turn nearly 90° to pass through turbines. The powerhouse of McNary Dam is oriented at right angles to the course of the River.

DESIGN AND OPERATION OF SAMPLING APPARATUS

A special intake frame supporting six fyke nets (fig. 4) was used to capture fingerlings passing through turbine intakes at The Dalles and McNary Dams. The fyke nets were installed one above the other in the frame. When the frame was installed in the intake, the nets extended from the ceiling of the intake to within 1 m. of the floor and strained the center flows of the intake. Nearly one-third of the flow of a single intake (one-ninth of the flow of a single turbine) was strained by the six nets, discounting slightly reduced flows through the nets owing to head loss caused by the webbing.

The frame was lowered through the intake gatewell (fig. 3) with a gantry crane operated by personnel of the U.S. Army Corps of Engineers. After the frame was installed, the turbine discharge was set. Normal fluctuations in total head on the turbine produced minor changes in turbine discharge during each test. Water velocities without the nets

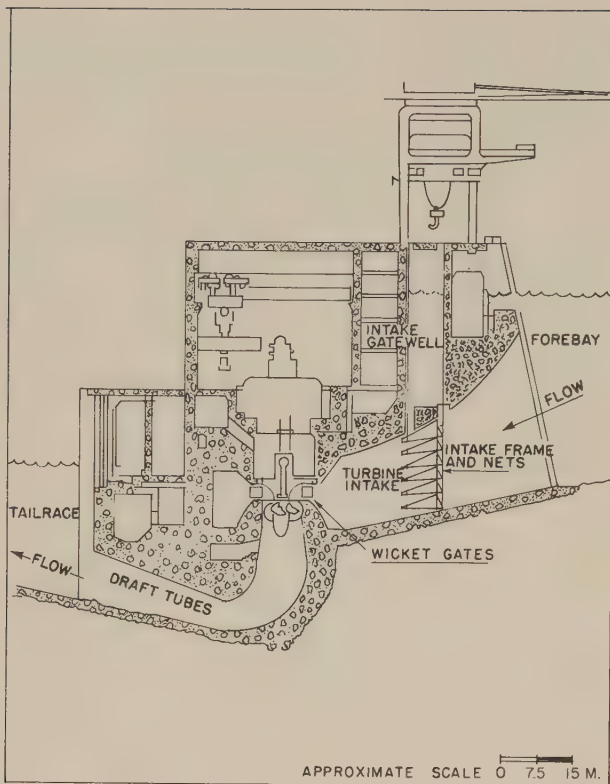


FIGURE 3.—Cross section of a main unit (turbine and associated water passages) at The Dalles Dam with intake frame in fishing position.

in place were almost the same throughout the zone strained by the nets, except for the normal boundary layer associated with the intake ceiling.⁴ Therefore, all nets strained about the same amount of water.

The uppermost net was placed on the frame so the top edge of the net mouth was aligned with the intake ceiling. The frame used at The Dalles Dam was equipped with a stationary fish-tight screen extending from the top edge of the net mouth to the upstream side of the frame to provide a partial block of the opening to the gatewell (fig. 5). At McNary Dam, the frame was equipped with a hinged screen as well as a stationary screen (fig. 5). Together, the screens formed a fish-tight barrier that blocked the entire opening to the gatewell upstream from the top net.

The nets at both Dams were 1.97 m. wide by 2.13 m. high at the mouth and were 5.79 m. long, includ-

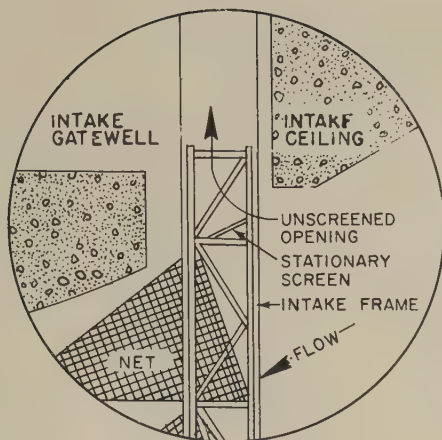
ing the cod end. Fyke nets at The Dalles Dam incorporated 12.7 mm. stretched mesh nylon webbing in the forward half of the body and 9.5 mm. stretched mesh nylon in the back half. At The Dalles, the smaller mesh tended to plug up with fine vegetable debris; the difficulty was alleviated at McNary Dam by constructing fyke nets entirely of 12.7 mm. stretched mesh. Cod ends of the nets at both Dams were of 3.2 mm. nylon bobbnet.

Procedure was the same at both Dams. Before the frame was lowered to fishing position, each net was folded and tied to the frame with string that could be broken easily by flows in the turbine intake. Flows were stopped before the frame was lowered or raised to prevent capture of fish while the nets were moving up or down. At the end of each fishing period, the intake frame was hauled to deck level, and the contents of each net were emptied into separate containers for sorting and counting.

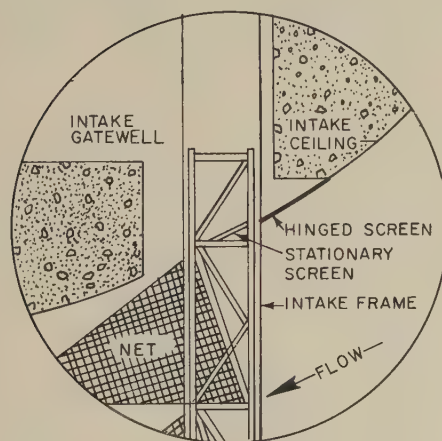


FIGURE 4.—Intake frame being lowered through gatewell into a turbine intake at McNary Dam. Frame supports fyke nets used to measure diel movement and vertical distribution of fingerling salmonids approaching Kaplan turbines.

⁴ Unpublished data furnished by U.S. Army Corps of Engineers, North Pacific Division, Water Control Branch, 921 SW. Washington, Portland, Oreg. 97205.



THE DALLES DAM



M^CNARY DAM

FIGURE 5.—Upper portions of intake frame in fishing position at The Dalles Dam and McNary Dam. Note hinged screen used at McNary Dam to ensure that fish near the ceiling of the intake did not escape the top net by swimming up into the gateway.

DESIGN OF EXPERIMENTS

Experiments at The Dalles Dam measured (1) diel movement and (2) vertical distribution of fingerling salmonids in the turbine intakes. An additional experiment provided information on the vertical distribution of fingerlings at McNary Dam.

THE DALLES DAM EXPERIMENTS

In both experiments at The Dalles Dam, the fyke nets were fished in the center intake (B) of turbines at both ends and at the middle of the part of the powerhouse that contained operating turbines. Turbines 1 to 10 operated continuously; tur-

bines 11 and 12 operated intermittently; turbines 13 through 22 had not been installed. At the beginning of each fishing period, the turbine was set to discharge about 310 c.m.s. (cubic meters per second), producing a water velocity of about 1.2 m.p.s. (meters per second) in the zone strained by the nets (measured without the nets in place). The gateway involved during a test was uncovered for the entire test period.

The salmonids were classified into two major size groups. Fish in the smaller group (under 80 mm. fork length) were termed O-group, or first year of life. Periodic examinations indicated this group was composed almost exclusively of juvenile chinook salmon (*Oncorhynchus tshawytscha*). Fish 80 mm. and longer were classed as I-group (second year of life or more) and identified by species. Catches of I-group salmonids during the experiment on diel movement included chinook salmon and steelhead trout (*Salmo gairdneri*). Ammocoetes of the Pacific lamprey (*Lampetra tridentata*) also were caught. Catches made during the study of vertical distribution included I-group sockeye salmon (*O. nerka*) in addition to the species mentioned above.

The first experiment (April 7–27, 1960) consisted of 18 tests to study diel movement of juvenile salmonids in turbine intakes. Each test was composed of one day- and one night-fishing period in the same intake within a single 24-hour period. Day fishing averaged 10¼ hours within the 12-hour period, 7 a.m. to 7 p.m. Night fishing averaged 10¼ hours within the 12-hour period, 7 p.m. to 7 a.m. Tests in each area of the powerhouse were made at 2- to 6-day intervals, conditions permitting. Five tests were made at unit 1, seven at unit 5, and six at units 10 and 11 (fig. 2).

In the second experiment (April 28 to May 12, 1960), 14 tests were made to sample the vertical distribution of fingerling salmonids. Each test was composed of a single fishing period, averaging 16 hours within the 17-hour period from 3:30 p.m. to 8:30 a.m.⁵ Tests were made in each of three areas of the powerhouse; five in unit 1, six in units 5 and 6, and three in units 10 and 12. Tests in a single area were spaced at least 3 days apart.

⁵ This fishing period was chosen to allow personnel of the U.S. Army Corps of Engineers to install and remove the intake frame without seriously disrupting their normal work schedule.

McNARY DAM EXPERIMENT

One set of 10 tests was completed at McNary Dam (April 24 to May 26, 1961) to determine the vertical distribution of juvenile salmonids. Each test covered a single 8-hour fishing period, beginning at 7 p.m. and ending at 5 a.m. Tests were run only in intake C of unit 12, which is near the center of the River channel. At the beginning of each test, the turbine discharge was set at 354 c.m.s., producing a water velocity of about 1 m.p.s. in the zone strained by the nets, as measured without the nets in place (footnote 4). Tests were run in pairs (2 consecutive days) with 6 nights between each pair. The gatewell was uncovered for the duration of the experiment.

The O-group salmonids were scarce; only I-group chinook and sockeye salmon and I-group steelhead trout were taken in sufficient numbers for analysis. Some ammocoetes were caught, but the data are not included here.

RELIABILITY OF CATCH DATA

Three major factors could have affected the reliability of the catch data: (1) different fishing efficiency of the fyke nets between day- and night-fishing periods, (2) capture of fish as the nets were drawn up through the water in the gatewells, and (3) avoidance of the top net at The Dalles Dam by fish that entered the gatewell before reaching the net.

Efficiency of the fyke nets could have varied if fish were able to see the nets better during the day than during the night. Recent experiments in the Snake River below Brownlee Dam indicated this possibility. Sims (unpublished)⁶ found that "scoop traps" were three times more efficient in capturing marked fish at night than during the day. Because vertical distribution of the fish was constant, he suggested that lessened visibility may have been responsible for the higher trap efficiencies at night. Illumination within the turbine intakes was not measured during tests reported here, but Secchi disc readings ranged from 0.43 to 0.85 m. at The Dalles Dam. In addition, the fyke nets were located within the turbine intake (about 15 m. downstream from the mouth) under more than 20 m. of water (vertical distance through the

water in the gatewell). The turbidity and the location of the nets indicated that illumination was probably not much higher during the day than during the night. It seems unlikely that fish were able to see the nets well during either day or night.

Recognizing that fish might be caught as the nets were drawn up through static water in the gatewells, I examined the physical condition of the fish to determine where they were caught. Prior experience had proven that fish would be dead and extensively descaled when caught by nets in water velocities equal to those in the turbine intakes. I reasoned that because water in the gatewell was not flowing, fish from nets raised slowly through the gatewell would be alive and suffer no more harm than would be caused by a dip net. Few live fish were taken during the experiment; when present, they were excluded from the catch data.

The catches made in the top net at The Dalles Dam may not have been indicative of the actual number of fish in that area because some may have escaped by swimming into the gatewell through the unscreened opening upstream from the net. Modifications of the intake frame precluded avoidance of the top net at McNary Dam.

Available information concerning the three points discussed in this section leads me to believe that the catch data depict reliably the general behavior of fish in turbine intakes. Experimental equipment and procedures that can circumvent these potential sources of error are nevertheless desirable for future experiments.

DIEL MOVEMENT

Data on diel movement of migrating juvenile salmonids in turbine intakes (intake B of units 1, 5, 10, and 11) at The Dalles Dam are presented in table 1. Occurrence by age groups and species is presented graphically in figure 6.

The following conclusions seem to be warranted:

1. Day and night passage for all age groups and species did not differ significantly among intakes sampled (at both ends and the middle of the row of operating turbines).

2. Although all age groups and species were more abundant at night than during the day, only the I-group salmonids were significantly more plentiful.

3. Of the I-group chinook salmon and I-group steelhead trout, 94 and 85 percent, respectively,

⁶ Sims, Carl W. Escapement of juvenile salmonids from Brownlee Reservoir. Fish-Passage Research Program, Bureau of Commercial Fisheries, Seattle, Wash. Manuscript in preparation.

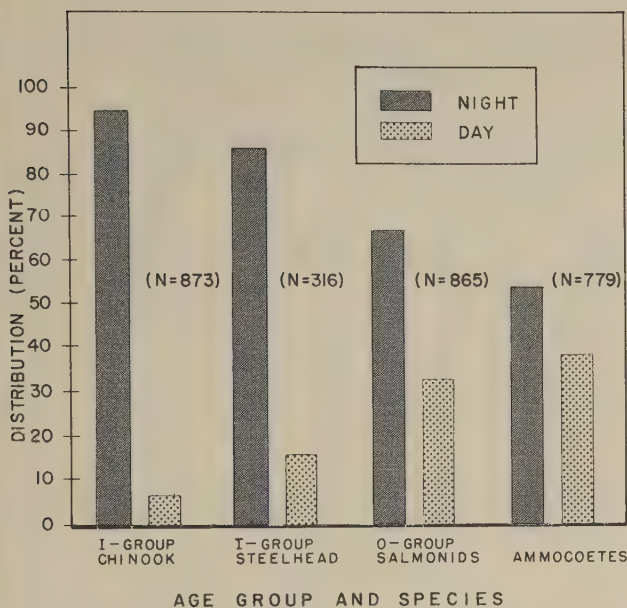


FIGURE 6.—Comparison of day (7 a.m. to 7 p.m.) and night (7 p.m. to 7 a.m.) catches of juvenile anadromous fish in turbine intakes of The Dalles Dam. Results of 18 tests, April 7-27, 1960.

TABLE 1.—Diel movement of fingerling salmonids and lamprey ammocoetes in turbine intakes of unit 1 (downstream end), unit 5 (center), and units 10 and 11 (upstream end of powerhouse) at The Dalles Dam

[Results of 18 tests, April 7-27, 1960]

Age groups and species	Catch by powerhouse area ¹								
	Downstream end			Middle			Upstream end		
	Night	Day	Total	Night	Day	Total	Night	Day	Total
I-group chinook salmon	94.4	5.6	358	94.2	5.8	189	93.9	6.1	326
I-group steelhead trout	89.8	10.2	118	82.7	17.3	127	81.7	18.3	71
O-group salmonids	61.2	38.8	201	62.5	37.5	248	71.7	28.3	416
Ammocoetes	63.5	36.5	315	51.1	48.9	282	75.8	24.2	182

¹ See figure 2 for location.

were caught at night. Of the O-group salmonids and ammocoetes, 67 and 62 percent, respectively, were caught at night.

Results reported here agree generally with those of other investigators of day and night movement of fingerlings. In the undammed sections of the Snake and Columbia Rivers, most of the I-group chinook salmon and I-group steelhead trout were captured from 6 p.m. to 6 a.m. (Mains and Smith, footnote 3). In research in special bypasses at Bonneville Dam, Gauley et al. (1958) found signifi-

cantly more O-group chinook salmon, I-group chinook salmon, and I-group steelhead trout migrating from 6 p.m. to 6 a.m. in 4 out of 5 seasons—1946, 1949, 1950, and 1953. More recently, Monan, McConnell, Pugh, and Smith (unpublished) ⁷ caught a majority of salmonid fingerlings (mixed species) between 8 p.m. and 6 a.m. in the Snake River.

VERTICAL DISTRIBUTION

Vertical distribution of juvenile anadromous fish migrating through turbine intakes of The Dalles Dam (intake B of units 1, 5, 6, 10, and 12) and of McNary Dam (intake C of unit 12) is presented in tables 2 through 8 and figures 7 and 8.

TABLE 2.—Vertical distribution of O-group salmonids in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth ¹	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	Number	Percent	Number	Percent	Number	Percent
1.....	0-2.1	88	30.4	111	31.6	107	24.6
2.....	2.3-4.4	42	14.5	70	19.9	93	21.4
3.....	4.6-6.7	41	14.2	49	14.0	76	17.5
4.....	6.9-9.0	43	14.9	63	18.0	81	18.7
5.....	9.2-11.3	32	11.1	40	11.4	62	14.3
6.....	11.4-13.6	43	14.9	18	5.1	15	3.5
Total.....		289	100.0	351	100.0	434	100.0

¹ From ceiling of intake at gateway.

TABLE 3.—Vertical distribution of I-group chinook salmon fingerlings in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth ¹	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	Number	Percent	Number	Percent	Number	Percent
1.....	0-2.1	321	55.9	211	45.8	51	35.2
2.....	2.3-4.4	131	22.8	113	24.5	46	31.7
3.....	4.6-6.7	62	10.8	67	14.5	29	20.0
4.....	6.9-9.0	25	4.4	36	7.8	13	9.0
5.....	9.2-11.3	17	3.0	24	5.2	5	3.4
6.....	11.4-13.6	18	3.1	10	2.2	1	.7
Total.....		574	100.0	461	100.0	145	100.0

¹ From ceiling of intake at gateway.

⁷ Monan, Gerald E., Robert J. McConnell, John R. Pugh, and Jim R. Smith. Distribution of downstream migrant salmonids and the study of debris in the Snake River above Brownlee Reservoir. Fish-Passage Research Program, Bureau of Commercial Fisheries, Seattle, Wash. Manuscript in preparation.

TABLE 4.—Vertical distribution of I-group steelhead trout fingerlings in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth ¹	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	Num- ber	Per- cent	Num- ber	Per- cent	Num- ber	Per- cent
1.....	0- 2.1	66	44.9	87	46.3	9	56.3
2.....	2.3- 4.4	39	26.6	51	27.1	3	18.7
3.....	4.6- 6.7	19	12.9	25	13.3	3	18.7
4.....	6.9- 9.0	9	6.1	18	9.6	0	0
5.....	9.2-11.3	8	5.4	3	1.6	1	6.3
6.....	11.4-13.6	6	4.1	4	2.1	0	0
Total.....		147	100.0	188	100.0	16	100.0

¹ From ceiling of intake at gateway.

TABLE 7.—Vertical distribution of fingerling salmonids in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth ¹	All species and age groups	
		Number	Percent
1.....	M. 0- 2.1	1,190	39.3
2.....	2.3- 4.4	695	22.9
3.....	4.6- 6.7	442	14.6
4.....	6.9- 9.0	345	11.1
5.....	9.2-11.3	217	7.2
6.....	11.4-13.6	140	4.6
Total.....		3,029	100.0

¹ From ceiling of intake at gateway.

TABLE 8.—Vertical distribution of fingerling salmonids in turbine intake 12-C at McNary Dam. Combined results of 10 tests extending from 7 p.m. to 5 a.m.

[Test period, April 24 to May 26, 1961]

Net number (top to bottom)	Depth ¹	Age group and species						Total	
		I-group chinook		I-group steelhead		I-group sockeye			
		M.	Number	Percent	Number	Percent	Number	Percent	Number
1-----	0- 2.1	351	56.7	47	54.0	104	33.6	502	49.4
2-----	2.3- 4.4	140	22.6	17	19.5	89	28.7	246	24.2
3-----	4.6- 6.7	74	12.0	16	18.4	46	14.8	136	13.4
4-----	6.9- 9.0	33	5.3	5	5.8	35	11.3	73	7.2
5-----	9.2-11.3	12	1.9	2	2.3	22	7.1	36	3.5
6-----	11.4-13.6	9	1.5	0	0	14	4.5	23	2.3
Total-----		619	100.0	87	100.0	310	100.0	1,016	100.0

¹ From ceiling of intake at gateway.

TABLE 5.—Vertical distribution of I-group sockeye salmon fingerlings in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth ¹	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	Num- ber	Per- cent	Num- ber	Per- cent	Num- ber	Per- cent
1.....	0- 2.1	70	36.6	52	26.1	17	50.0
2.....	2.3- 4.4	47	24.6	54	27.2	6	17.6
3.....	4.6- 6.7	31	16.2	37	18.6	3	8.8
4.....	6.9- 9.0	20	10.5	33	16.6	4	11.8
5.....	9.2-11.3	15	7.9	8	4.0	2	5.9
6.....	11.4-13.6	8	4.2	15	7.5	2	5.9
Total.....		191	100.0	199	100.0	34	100.0

¹ From ceiling of intake at gateway.

TABLE 6.—Vertical distribution of lamprey ammocoetes in turbine intakes of The Dalles Dam. Combined results of 14 tests extending from 3:30 p.m. to 8:30 a.m.

[Test period, April 28 to May 12, 1960]

Net number (top to bottom)	Depth ¹	Catch by powerhouse area					
		Downstream end		Middle		Upstream end	
	M.	Num- ber	Per- cent	Num- ber	Per- cent	Num- ber	Per- cent
1.....	0- 2.1	52	8.0	36	4.9	13	4.4
2.....	2.3- 4.4	98	15.1	92	12.4	19	6.5
3.....	4.6- 6.7	128	19.7	142	19.3	41	14.0
4.....	6.9- 9.0	154	23.7	171	23.2	62	21.2
5.....	9.2-11.3	167	25.8	204	27.7	89	30.4
6.....	11.4-13.6	50	7.7	92	12.5	69	23.5
Total.....		649	100.0	737	100.0	293	100.0

¹ From ceiling of intake at gateway.

Catches at The Dalles Dam showed:

1. Vertical distribution of salmonids did not vary among areas of the powerhouse sampled; therefore, the catch data for all intakes were combined for subsequent analysis.

2. The combined catches of all salmonid species and age groups showed that most were caught in the top two of the six nets.

3. The I-group chinook salmon and I-group steelhead trout were most strongly concentrated in the top two nets—73 and 74 percent, respectively.

4. The O-group chinook salmon and I-group sockeye salmon were less strongly concentrated in the top two nets—48 and 58 percent, respectively.

5. The vertical distribution of ammocoetes was the reverse of that of salmonids; very few were caught in the top two of the six nets. This distribution held for all areas of the powerhouse. The zone of highest concentration at the upstream end

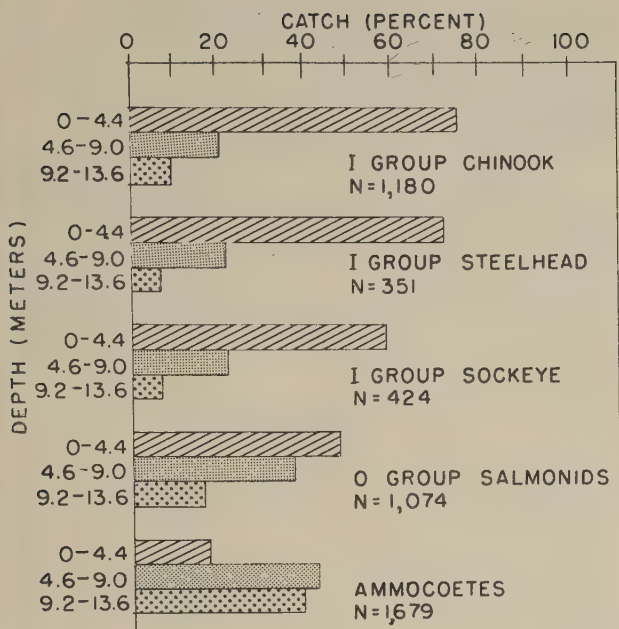


FIGURE 7.—Combined results of 14 tests showing vertical distribution of juvenile anadromous fish in turbine intakes of The Dalles Dam. Each 16-hour test was between 3:30 p.m. and 8:30 a.m. Test period, April 28 to May 12, 1960.

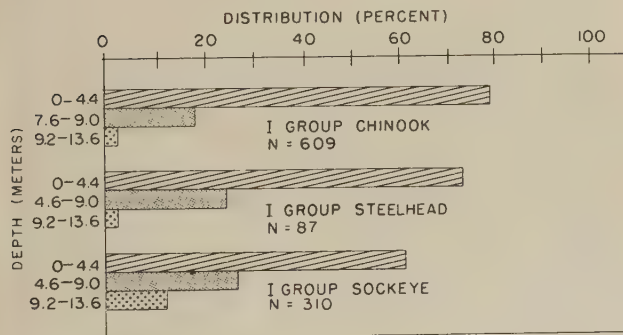


FIGURE 8.—Combined results of 10 tests showing vertical distribution of fingerling salmonids in intake 12-C at McNary Dam. Each 8-hour test was between 7 p.m. and 5 a.m. Test period, April 24 to May 26, 1961.

of the powerhouse occurred in the bottom two of the six nets, whereas the zone of highest concentration was in the two center nets in the center and downstream end of the powerhouse. This difference was statistically significant.

Catches at McNary Dam showed that the vertical distribution of I-group chinook and sockeye salmon and I-group steelhead trout was much

the same as the vertical distribution of these age groups and species at The Dalles Dam. The I-group chinook salmon and steelhead trout were most strongly concentrated in the top two nets (79.3 and 73.5 percent, respectively), whereas I-group sockeye salmon were somewhat less concentrated (62.3 percent).

IMPLICATIONS OF RESEARCH IN TURBINE INTAKES

Information on diel movement and vertical distribution of fingerling salmonids in turbine intakes applies directly to the problem of developing methods for reducing fingerling mortality in Kaplan turbines. Important implications are discussed below.

DIEL MOVEMENT

According to past research, day and night movement of fish can vary significantly from year to year, presumably because of changes in turbidity and other facets of water quality. Mains and Smith (footnote 3) caught 57 percent of the I-group chinook salmon at night in the Snake River in 1954, whereas in 1955 they caught 78 percent at night. Gauley et al. (1958) caught significantly more O-group chinook salmon and I-group steelhead trout in special bypasses at Bonneville Dam during the night in 4 of 5 seasons; but in 1952, significantly more of these species were caught by day. Data by Gauley et al. (1958) suggested that turbidity may have influenced timing of fish movement. In view of past research, the data on day and night movement reported here should be applied with some reservation because continuing development of the river system may well alter water quality, including turbidity, in the future.

Although data on day and night movement must be considered only partially complete, the results—especially for I-group fingerlings—suggest a fortunate relation between timing of fish passage at dams and the normal schedule of turbine loading. Night movement of fish through turbines favors higher rather than lower average survival. At night the decreased demand for power causes reduced turbine loads. Preliminary information recently obtained at Big Cliff Dam⁸ indi-

⁸ Oligher, Ray. Fish passage through turbines—tests at Big Cliff hydroelectric plant. U.S. Army Corps of Engineers, North Pacific Division, Walla Walla District, Walla Walla, Wash. Letter report (1965), 14 pp.

cates that survival is highest at highest turbine efficiencies. Peak efficiency is achieved at reduced turbine loads, typically near 70 percent of maximum rated capacity.⁹

Reduced power demand also increases flexibility for adjusting turbine loads to maximize fish survival—shifting of load demand from turbines where fish passage is high to turbines where fish passage is low (between turbines in a given dam and between dams in the same power-grid system). The potential increase in fish survival that might be achieved by using this technique, however, cannot be estimated with accuracy from available data. Among other requirements, timing of fish movement should be determined for shorter periods of time, especially for dawn and dusk. Peaks are expected at dawn and dusk (Mains and Smith, footnote 3; Gauley et al., 1958; Monan et al., footnote 7) and the demand for power fluctuates during these hours of the day.

VERTICAL DISTRIBUTION

Data on vertical distribution have helped define more precisely the direction that future research should take to develop suitable protective methods. Most fingerlings in turbine intakes of both The Dalles Dam and McNary Dam are in flows near the ceiling of the intake. These flows pass the turbine blades at or near the hub (G. D. Johnson, footnote 2). If fish remain in these flows, they also must pass the blades near the hub. Protective methods designed to eliminate or nullify the effects of lethal agents, therefore, should be used first at the hub of the runner. These data also imply that most salmonid fingerlings could be routed into safe bypasses if a guiding system were designed to remove fish only from the upper 4.6 m. of water within turbine intakes.

SUMMARY

1. A frame supporting six fyke nets was used to measure diel movement and vertical distribution of fingerling chinook salmon, sockeye salmon, steelhead trout, and ammocoetes of the Pacific lamprey in turbine intakes at The Dalles Dam (1960) and McNary Dam (1961).

2. The nets were positioned one above the other

in the frame and extended from the intake ceiling to within 1 m. of the floor to strain the center third of flows in a single intake (one-ninth of total turbine discharge).

3. Diel movement for all age groups and species did not differ significantly between areas of the powerhouse at The Dalles Dam. Although all age groups and species were more abundant at night (7 p.m. to 7 a.m.) than during the day (7 a.m. to 7 p.m.), only the I-group salmonids were significantly so. The night catches of I-group chinook salmon and I-group steelhead trout were 94 and 85 percent of the total, respectively, whereas the night catches of O-group salmonids and ammocoetes were 67 and 62 percent of the total, respectively.

4. Vertical distribution of salmonids did not vary between areas of the powerhouse sampled at The Dalles Dam. At both Dams, most I-group fingerlings were concentrated in the top two of six nets, or within 4.6 m. of the ceiling of the turbine intakes. At The Dalles and McNary Dams, respectively, the results for I-group chinook salmon were 73 and 79.3 percent; for I-group steelhead trout, 74 and 73.5 percent; and for I-group sockeye salmon, 58 and 62.3 percent. O-group salmonids were less strongly stratified than I-group fingerlings; 48 percent were caught in the top two nets.

5. Vertical distribution of ammocoetes at The Dalles Dam was the reverse of that for salmonids; few were taken in the top two nets.

6. Predominantly night movement of fingerlings through turbines favors higher rather than lower survival because (a) survival is highest at reduced loads near 70 percent of maximum rated capacity and (b) reduction in demand for power at night results in lower turbine loads. Reduced turbine loads also make it possible to shift loads from turbines where fish passage is greatest to those where fish passage is least, thus increasing total fish survival.

7. The concentration of fingerlings near the ceilings of intakes implies that most fish pass through the Kaplan runners at or near the hub. It follows that methods for eliminating the effects of lethal agents at the runner should be applied first at the hub. In addition, use of deflection and bypass techniques near intake ceilings would be advantageous because the concentration of fish is greatest in this region.

⁹ Hydraulic plant operator training manual, Part II, U.S. Army Corps of Engineers, North Pacific Division, Portland, Ore. 22 pp.

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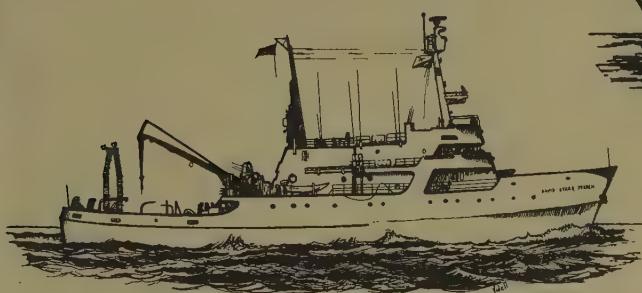
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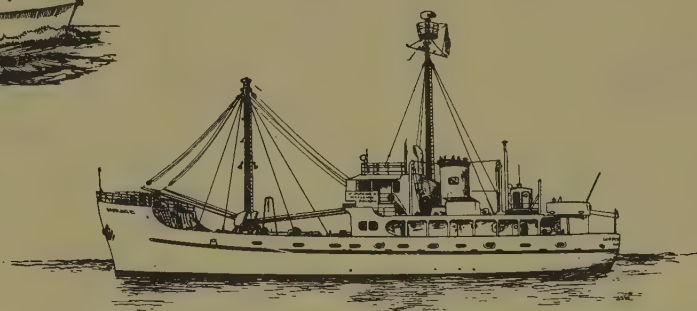
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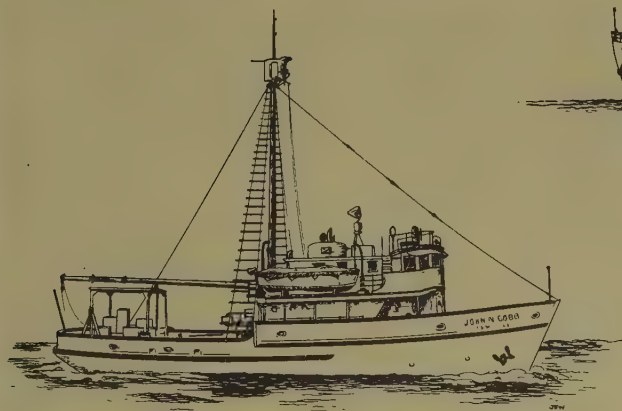
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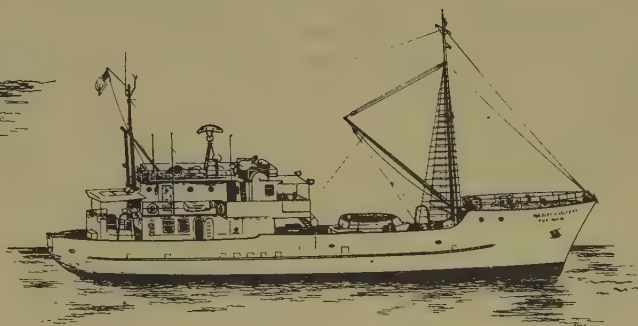
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CONTENTS

FISHERY BULLETIN OF THE U.S. FISH AND WILDLIFE SERVICE VOLUME 66, NUMBER 3

	Page
Models of oceanic migrations of Pacific salmon and comments on guidance mechanisms. By William F. Royce, Lynwood S. Smith, and Allan C. Hartt. (Published March 1968.) -----	441
Hydrological and biological characteristics of Florida's west coast tributaries. By Alexander Dragovich, John A. Kelly, Jr., and H. Grant Goodell. (Published March 1968.)-----	463
Intragravel flow and interchange of water in a streambed. By Walter G. Vaux. (Published March 1968.)-----	479
Mortality rates in populations of pink shrimp, <i>Penaeus duorarum</i> , on the Sanibel and Tortugas grounds, Florida. By T. J. Costello and Donald M. Allen. (Published March 1968.)-----	491
Oceanographic conditions in the northeast Pacific Ocean and their relation to the albacore fishery. By Robert W. Owen, Jr. (Published March 1968.)-----	503
Calanoid copepods from the central north Pacific Ocean. By Tai Soo Park. (Published March 1968.)-----	527
A rapid method of tagging fish. By Henry M. Sakuda. (Published March 1968.)-----	573
Migration and distribution of pink salmon spawners in Sashin Creek in 1965, and survival of their progeny. By William J. McNeil. (Published May 1968.)-----	575
Preliminary analysis of the catch curve of the Pacific sardine, <i>Sardinops caerulea</i> Girard. By Sigeiti Hayasi. (Published May 1968.)-----	587
Diel movement and vertical distribution of juvenile anadromous fish in turbine intakes. By Clifford W. Long. (Published May 1968.)-----	599

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